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A comprehensive assessment of ship-mediated invasion risk in the Canadian Arctic

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A COMPREHENSIVE ASSESSMENT OF SHIP-MEDIATED INVASION RISK IN THE CANADIAN ARCTIC

by

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A COMPREHENSIVE ASSESSMENT OF SHIP-MEDIATED INVASION RISK IN THE CANADIAN ARCTIC

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DECLARATION OF CO-AUTHORSHIP / PREVIOUS PUBLICATION

I. Co-Authorship Declaration

I hereby declare that this dissertation incorporates material that is the result of joint research. H.J. MacIsaac and S.A. Bailey contributed to all chapters by providing opportunities and facilities necessary to complete the research along with intellectual guidance. In Chapter 2, C.J. Wiley contributed by providing data and commenting on the manuscript. E. Briski contributed to Chapters 3 and 5 by providing detailed guidance and helpful direction. In Chapter 5, J.N. Bradie provided statistical assistant and comments on the text. N. Simard also contributed to Chapter 5 by providing data and helpful comments. In all cases, the key ideas, data interpretation, and writing of all chapters were performed by the author, Farrah T. Chan.

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II. Declaration of Previous Publication

This dissertation includes four original papers that have been previously published/submitted for publication in peer-reviewed journals, as follows:

Dissertation chapter	Publication title/full citation	Publication status
Chapter 2	Chan FT, Bailey SA, Wiley CJ, MacIsaac HJ (2013) Relative risk assessment for ballast-mediated invasions at Canadian Arctic ports. Biological Invasions 15:295-308	Published
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Chapter 5	Chan FT, Bradie J, Briski E, Bailey SA, Simard N, MacIsaac HJ. Assessing introduction risk using species' rank-abundance distributions. Proceedings of the Royal Society B	In revision

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ABSTRACT

Ships' ballast water and hull fouling are leading transport vectors of aquatic nonindigenous species (NIS) globally, yet very few studies have examined the magnitude of these vectors in the Arctic. A combination of climate warming, resource exploration, and expanded Arctic shipping is expected to increase the risk of introducing NIS to the Arctic via ship vectors. Therefore, a formal assessment of the current risk levels associated with these vectors is warranted. I conducted a vector-based risk assessment to identify ports at relatively high risk of ballast-mediated invasions and the responsible vessel pathway. Churchill appears to be at greatest invasion risk from ballast water discharged by international merchant vessels. I subsequently collected ballast water and hull fouling samples from 32 and 13 ships, respectively, at Churchill and quantified colonization pressure (CP) and total propagule pressure (total PP) associated with each vector. I evaluated relative arrival potential of invertebrates via ballast water by comparing CP, total PP, and the relationship between CP and total PP in vessels from Europe destined for the Arctic with those bound for Atlantic Canada and the Great Lakes. Arrival potential of invertebrates in ballast water of Arctic ships may be lower than that of Atlantic ships but similar to that of Great Lakes ones. Furthermore, I determined the relative importance of ballast water and hull fouling as transport vectors of NIS to the Canadian Arctic by comparing CP, total PP, number of NIS, and total abundance of all NIS for invertebrates transported by each vector. Hull fouling appears to be the more important transport vector of NIS. Finally, to better understand ship-mediated dispersal mechanisms, I examined temporal changes in characteristics of species assemblages

entrained by ballast water using datasets from other, previously studied Canadian systems with large sample size. Rank-abundance distributions and CP:total PP patterns varied widely by voyage route (Pacific vs. Atlantic), taxonomic group (invertebrates, diatoms, and dinoflagellates), and ballast water management (control vs. exchanged). Results of this dissertation can help direct research and management efforts at high-risk ports as well as the vector and vessel pathways that pose the greater risk given limited managerial resources.

DEDICATION

To my parents, Fong and Christopher Chan,

for their loving support and consistent encouragement.

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CHAPTER 1: GENERAL INTRODUCTION

Human-mediated nonindigenous species (NIS) introductions have been recognized as a key component of global change (Ricciardi 2007; Wilson et al. 2009; Simberloff et al. 2013). Human activities such as the aquarium trade (Rixon et al. 2005), horticulture (Reichard and White 2001), and commercial shipping (Seebens et al. 2013) are transforming natural ecosystems by transporting NIS across geographic barriers to habitats beyond their native range. While some NIS are beneficial, such as food crops and aquaculture species, many others have detrimental effects on recipient environments, including hybridization with resident populations, local extirpations and global extinctions of native species, disruption of ecosystem functions, enhanced transmission of viruses and pathogens, and substantial damage to natural resources and ecosystem services (e.g. Ricciardi and MacIsaac 2011; Simberloff et al. 2013; Paolucci et al. 2013; Blackburn et al. 2014).

1.1 Conceptual framework of biological invasions

Invasions occur as a multi-stage process consisting of uptake, transport, arrival, survival, establishment, and spread (Kolar and Lodge 2002; Colautti et al. 2006; Blackburn et al. 2011). At each stage, physical, chemical, and/or biological barriers serve to preclude invading NIS from transitioning to the next stage (Colautti et al. 2006; Blackburn et al. 2011). Propagules of one or more NIS must first be picked up and translocated by a transport vector from their source region to a new area, where they then must be introduced alive. Next, the propagules must survive ambient environmental

conditions and establish a self-sustaining population in their new habitat, where biological interactions may impede or facilitate establishment. Finally, the established population may proliferate and spread from the site of introduction. Failure of an invasion can occur at any of the stages; NIS must succeed at all stages in order to become invasive (Simberloff et al. 2009). The probability of NIS overcoming all stages of this process (i.e. probability of introduction) and the magnitude of consequences is referred to as invasion risk (Orr 2003).

A number of factors have been proposed to influence invasion risk, including characteristics of potential NIS, features of recipient communities, propagule pressure (PP), and colonization pressure (CP) (Catford et al. 2009). Characteristics such as *r*-selected traits, polyphagy, high dispersal rate, broad physiological tolerance, high genetic variability, high phenotypic plasticity, and ability to adjust behavioural responses to novelties have been identified as common attributes of successful NIS (e.g. Elton 1958; Kolar and Lodge 2001; Richards et al. 2006; Thuiller et al. 2006; Higgins and Richardson 2014; Liebl and Martin 2014). Communities that are vulnerable to invasion tend to have environmental conditions matching those of native habitat of invading NIS, high environmental heterogeneity, low species diversity, absence of natural enemies (i.e. predators, competitors, and pathogens), and a history of habitat disturbance (e.g. Lozon and MacIsaac 1997; Tilman 1997; Levine et al. 2004; Herborg et al. 2007; Melbourne et al. 2007). However, a number of theoretical and empirical studies have demonstrated that invasion risk is affected more by propagule supply (i.e. PP and CP) than by species- and community-based attributes (e.g. Lockwood et al. 2005; Von Holle and Simberloff 2005; Colautti et al. 2006; Simberloff 2009; Blackburn et al. 2013). It could be argued that if a

NIS cannot reach a new habitat, then physical, chemical, and/or biological properties of the recipient environment are irrelevant. PP is a measure of the number of introduction events combined with the number of propagules released per event, and has been shown to strongly influence invasion risk (Colautti et al. 2006; Simberloff 2009; National Research Council 2011). High PP enhances probability of population establishment by decreasing demographic and environmental stochasticity (Lockwood et al. 2005; Taylor and Hastings 2005; Simberloff 2009). Similarly, CP (i.e. the number of species released) is a determinant of invasion risk when multiple species are introduced to given area, because greater CP increases the likelihood that at least one species will form a self-sustaining population in the new environment (Chiron et al. 2009; Lockwood et al. 2009).

Many transport vectors such as ships' ballast water or fouled hulls, bait worm packaging, and wood dunnage often inadvertently transport and introduce large, mixed-species assemblages during a single human-mediated movement (e.g. Briski et al. 2013; Haack et al. 2014; Haska et al. 2014). To characterize invasion risk for these introductions, researchers have recently begun to explore the relationship between CP and PP or between CP and total PP (i.e. PP of all species combined) for assemblages entrained by transport vectors (e.g. Lockwood et al. 2009; Briski et al. 2013; Villac et al. 2013). If species introduction is a random sampling process, CP should be positively related to PP because a larger sample size is expected to include more species than a smaller one (Lockwood et al. 2009). The strength of the CP:PP relationship may, however, depend on numerous factors including the nature of the vector, composition of source community, duration of transport, and taxonomic group (Lockwood et al. 2009; Briski et al. 2012a, 2014). Furthermore, because species vary in their abundances, species

rank-abundance distributions have been proposed as a means to characterize invasion risk associated with multi-species transport vectors (Briski et al. 2014; Drake et al. 2014). Rank abundance distributions, constructed by plotting species abundance on the y-axis versus ranked abundance on the x-axis, are useful to visualize relative abundance of species in a community (McGill et al. 2007).

1.2 Climate change and biological invasions

Recent studies demonstrate that climate change may have synergistic effects on the rate and extent of biological invasions (e.g. Walther et al. 2009; Bellard et al. 2013; Floerl et al. 2013). Changes in temperature regimes, ocean currents, sea ice extent, and other key physical processes may facilitate invasions by promoting both natural and human-mediated species dispersal, enhancing survival and establishment of NIS in previously unsuitable areas, and amplifying impacts of established NIS in recipient communities (Hellmann et al. 2008; Vermeij and Roopnarine 2008; Post et al. 2009).

Interacting effects of climate change and biological invasions may be most profound in the Arctic, because annual temperature is increasing at approximately twice the global rate and future increases are projected to be severe (Cheung et al. 2009; Post et al. 2009; Wassmann et al. 2011; IPCC 2014). Climate-induced northern range expansion (e.g. capelin *Mallotus villosus* and killer whales *Orcinus orca*), and trans-Arctic dispersal (e.g. Pacific diatom *Neodenticula seminae*) have been observed in high-latitude waters in recent years (Reid et al. 2007; Higdon and Ferguson 2009; Provencher et at. 2012; Miettinen et al. 2013). The potential for human-mediated transport of NIS into the Arctic via activities such as shipping, resource exploration, and tourism is expected to increase as sea ice retreats, opening waterways and shipping channels and increasing accessibility

to the region (Miller and Ruiz 2014). Furthermore, present climatic conditions in certain high-latitude systems are already suitable for temperate species, thus successful establishment may be possible given sufficient propagule supply (de Rivera et al. 2011). Further changes in ocean conditions will enhance environmental similarity between Arctic and temperate habitats, thereby increasing vulnerability of Arctic ecosystems to NIS invasions (Ware et al. 2013).

1.3 Commercials ships as transport vectors

Ships provide at least two important vectors for the transport of aquatic NIS (Carlton 1985; Fofonoff et al. 2003a; Hewitt et al. 2009). The first is ballast water, which is carried by vessels to accommodate changes in cargo weight and to provide stability and trim. A wide variety of species (i.e. substantial CP and PP), including bacteria, phytoplankton, zooplankton, benthic invertebrates, and fish, may be loaded with ballast water at the source port and discharged at subsequent ports-of-call (e.g. Carlton 1985; Simard et al. 2011; Briski et al. 2013). A second vector is the exterior of vessel surfaces. Many benthic, sessile and mobile species (i.e. again, with low to high CP and PP) foul hull surfaces and can dislodge and/or reproduce at later ports (e.g. Davidson et al. 2009; Sylvester et al. 2011; Chapman et al. 2013). Given that commercial vessels transport more than 90% of the world's cargo, they provide extensive opportunities for translocation of aquatic NIS (Hulme et al. 2009). Indeed, ships are by far the most important transport vectors of aquatic NIS globally (Ruiz et al. 1997; Molnar et al. 2008; Williams et al. 2013). Consequently, mid-ocean ballast water exchange (BWE) has been implemented in many countries, including Canada, as a measure to reduce the probability of arrival of NIS by ballast water (IMO 2004; Government of Canada 2006). The

procedure replaces ballast water loaded at ports with oceanic water, reducing the abundance of propagules by purging most individuals and killing remaining ones via salinity shock (Bailey et al. 2011). BWE appears highly effective in reducing invasion risk for freshwater systems (Gray et al. 2007; Bailey et al. 2011), but its efficacy is mixed for marine habitats (Taylor et al. 2007; Cordell et al. 2009; Roy et al. 2012). Similarly, hull fouling may be managed via hull husbandry practices such as application of anti-fouling coatings and physical removal of fouling organisms using brushes, scrapers, or high-pressure blasting (Piola et al. 2009; Woods et al. 2012). Antifouling coatings, however, have a limited service life (one to five years) and do not provide effective protection to all parts of the hull (Piola et al. 2009). In some cases, hull cleaning may actually increase invasion risk by dislodging organisms into port environments (Woods et al. 2012).

1.4 Ship-mediated NIS in the Canadian Arctic

Canada has the longest coastline (202,080 km) in the world, the majority (80%) of which is located in Arctic waters (DFO 2014). The Canadian Arctic is home to some 120,000 residents, who are dependent on shipping for delivery of food, clothing, equipment, materials, and fuels (McCalla 1994). Commercial shipping also plays an important role in transporting natural resources (e.g. grain and nickel concentrates) from the Canadian Arctic to domestic and international markets (Niimi 2007). Shipping activities are expected to increase substantially in the near future owing to mineral, offshore oil and gas, offshore energy, infrastructure, and tourism development projects that have been planned for the area (Gavrilchuk and Lesage 2014).

To date, there has been no ship-mediated NIS reported from the Canadian Arctic. A nonindigenous alga *Dumontia contorta* has been recorded in Canada's Arctic waters, but the mechanism of its introduction is unknown (Mathieson et al. 2010). In comparison, more than 10 aquatic NIS have been found in other Arctic and sub-Arctic regions, although information on the mode(s) of transportation and long-term establishment conditions are generally not well documented (e.g. Streftaris et al. 2005; Ruiz and Hewitt 2009; Thorarinsdottir et al. 2014). The relatively small number of NIS reported in the Arctic may stem from the limited number of studies conducted there (Goldsmit et al. 2014), or to limited propagule supply (i.e. low CP and PP), as the extent of shipping to most northern ports has historically been low compared to temperate and tropical locations (Ruiz and Hewitt 2009).

A combination of warming climate and expanded Arctic shipping will increase the vulnerability of Canada's Arctic coastal ecosystems to ship-mediated invasions. Therefore, an evaluation of the potential for ballast water and hull fouling as transport vectors of NIS into the Canadian Arctic is clearly needed.

1.5 Dissertation objectives

This dissertation describes the first comprehensive assessment of ship-mediated invasion risk in the Canadian Arctic. First, I examine all stages of the invasion process in an *ex ante* risk assessment to identify Arctic ports at highest risk of NIS invasions via ballast water discharge. Next, focusing on the first stage of the invasion process, I quantify CP and PP delivered to the region by characterizing the composition of biota transported in ballast water and on hulls of vessels travelling to Canada's North. Finally, in a broader context, I explore how characteristics of species assemblages entrained by a

transport vector changes during transportation. Results of this study can improve present knowledge of the characteristics and mechanisms of human-assisted transport of NIS, thereby facilitating better understanding and management of biological invasions.

In chapter two, I develop a vector-based, predictive framework to assess relative invasion risk for unknown species assemblages transported in ballast water for the Canadian Arctic. The framework estimates the probability of NIS successfully transiting all stages of the invasion process and the magnitude of potential consequence based on ballast water discharge patterns, environmental similarity between ballast water source and recipient ports, and the number of high-impact NIS in connected source regions. Using this framework, I identified ports at greatest risk of ballast-mediated invasions and the corresponding shipping pathways for the Canadian Arctic.

In chapter three, I evaluate arrival potential of invertebrates via ballast water by examining CP, total PP, and the relationship between CP and total PP in vessels from Europe destined for the Arctic as compared to those bound for Atlantic Canada and the Great Lakes. For each shipping route, I also explore whether CP and/or total PP are influenced by transit factors such as temperature change and ballast water age, variables reported important in earlier studies (e.g. Cordell et al. 2009; National Research Council 2011; Brisk et al. 2013).

In chapter four, I conduct a quantitative evaluation of hull fouling and ballast water to determine their relative importance as transport vectors of NIS to the Canadian Arctic. I compare CP, total PP, nonindigenous CP (i.e. number of NIS), and nonindigenous total PP (i.e. total abundance of all NIS) for invertebrates transported on hulls versus those in ballast water. Additionally, I investigate fouling patterns across various ship sub-surfaces

(e.g. main hull, rudder, propeller) and explore the effects of maintenance practices and voyage history on the extent of vessel biofouling.

In chapter five, I examine temporal changes in characteristics of species assemblages entrained by ballast water. I use datasets from other, previously studied Canadian systems with larger sample size (i.e. Atlantic and Pacific coasts) to better understand the mechanism of ship-mediated dispersal. I used rank-abundance distributions and CP:total PP relationship as extensions of traditional summary statistics such as CP and total PP in order to assess introduction risk. Specifically, I test whether changes in assemblage structure and CP:total PP during transportation are the same for different voyage routes (Pacific vs. Atlantic), different taxonomic groups (invertebrates, diatoms, and dinoflagellates), or in response to ballast water management (control vs. exchanged). Findings of this chapter improve the understanding of human-mediated species dispersals and are likely transferable to Arctic shipping.

Finally, in chapter six, I briefly summarize the novel contributions made by this dissertation, and discuss the potential of ballast water and hull fouling as transport vectors of NIS to the Canadian Arctic.

CHAPTER 2: RELATIVE RISK ASSESSMENT FOR BALLAST-MEDIATED INVASIONS AT CANADIAN ARCTIC PORTS[1]

2.1 Introduction

Globalization has increased international trade and transport networks, moving not only people and goods but also nonindigenous species (NIS) around the world (Hulme 2009). While some NIS are introduced intentionally as biocontrol agents or food, many are transported and released accidentally as contaminants or stowaways (Hulme et al. 2008). Given the ecological and economic harm that may result from NIS introductions, considerable effort has been invested in developing risk assessments to direct NIS prevention and control strategies.

In the context of biological invasions, risk assessments quantify the probability and consequence of NIS introduction events (Hayes 2003). The majority of risk assessments have been conducted for single (e.g. Stone et al. 1997; Bartell and Nair 2003; Therriault and Herborg 2007) or selected few target species (e.g. Pheloung et al. 1999; Kolar and Lodge 2002; Barry et al. 2008). A typical species-specific risk assessment estimates the probability that a NIS will successfully pass through all stages of the invasion process and characterizes the expected impact of the species in the recipient environment. Invasion stages include arrival, survival, establishment, and spread, and may be evaluated individually before being combined into a final probability of successful introduction (Orr 2003). Completing a species-specific risk assessment requires extensive data on the

[1] Chan FT, Bailey SA, Wiley CJ, MacIsaac HJ (2013) Relative risk assessment for ballast-mediated invasions at Canadian Arctic ports. Biological Invasions15:295-305

invasion history, environmental requirements, and biological traits of target species, as well as characteristics of the recipient environment. Risk assessments may be performed prior to the introduction of a NIS in an effort to manage or regulate activities that may lead to the introduction; alternatively, they may be conducted retrospectively so that limited resources can be most effectively allocated to control or eradicate NIS already introduced (Andersen et al. 2004).

Recently, there have been several proposals to move toward vector-based risk assessment as a strategy for managing NIS (e.g. Andow 2003; Ruiz and Carlton 2003; Hulme 2009). A vector is defined as the conveyance carrying species along a pathway, where the pathway is the geographic route between the source region and the release sites (Lockwood et al. 2007). There are multiple reasons to conduct vector-based rather than species-specific risk assessments. First, it is often impossible to predict which species may be accidentally introduced via multi-species vectors, such as ballast water, shipping containers, and commercial imports (Andow 2003; Ruiz and Carlton 2003; National Research Council 2011). Second, biological and ecological data required for species-specific risk assessments are often limited even for priority high-risk NIS (Ruiz and Carlton 2003). Therefore, focusing efforts to characterize propagule pressure (i.e. the number of arrivals, the number of propagules per arrival, and the condition of the released propagules) and colonization pressure (i.e. the number of species) exerted by a transport vector to a given recipient area is a useful strategy for quantifying and predicting invasion risk (Colautti et al. 2006; Lockwood et al. 2009). In addition, results from vector-based risk assessments can be translated to vector management policies, such as the prohibition of high-risk species in the aquarium trade and mandatory ballast water

exchange in international shipping (Andow 2003). By addressing the vector, the entire assemblage of species associated with it is simultaneously managed, providing a powerful and efficient management approach (Ruiz and Carlton 2003).

Ballast water is a major transport vector of a wide variety of aquatic NIS worldwide (Klein et al. 2010; DiBacco et al. 2012; Seiden et al. 2011; Briski et al. 2013). Very few studies, however, have examined the magnitude of the vector in the Arctic (e.g. McGee et al. 2008; Ruiz and Hewitt 2009), and only one has done so qualitatively for northern Canada (Niimi 2007). At first glance, the Arctic would appear an unlikely region for ship-mediated biological invasions. The extent of shipping to most northern ports is low relative to temperate and tropical locations, thereby constraining the transfer of NIS. In addition, low temperature and limited food resources may hinder survivorship, reproduction, and/or population growth of many species in the Arctic (Vermeij and Roopnarine 2008; Ruiz and Hewitt 2009). However, changes in temperature regimes, ocean currents, sea level, and other key physical processes associated with climate change are expected to profoundly influence species dispersal and survival (Vermeij and Roopnarine 2008; Hellman et al. 2008; Ruiz and Hewitt 2009; Wassmann et al. 2011). For example, the Pacific diatom *Neodenticula seminae* was found in the North Atlantic Ocean for the first time since the Pleistocene (Reid et al. 2007). Evidence suggests that the species was likely carried by increased flows of Pacific water from the Bering Sea through the Arctic Ocean following recession of coastal ice sheets, however the possibility of ballast water transport could not be dismissed (Reid et al. 2007). Melting sea ice can facilitate human-mediated transport of NIS to the Arctic by opening new waterways and shipping channels in the Arctic Ocean as well as extending the length of

the shipping season (Howell and Yackel 2004; Arctic Council 2009; Khon et al. 2010). Once released in Arctic waters, NIS may benefit from enhanced survival associated with warmer climate and increased food supply (Vermeij and Roopnarine 2008; Cheung et al. 2009; Rooney and Paterson 2009).

Commercial vessels began to use the Northeast Passage and the Northern Sea Route in 2009 to dramatically reduce the time and cost to ship goods from northern Europe to northeast Asia and northwest North America (Khon et al. 2010). The Northwest Passage was free of pack ice and fully navigable in the summer of 2007, providing a direct shipping route between western Europe and eastern Asia for the first time in recorded history (Cressey 2007; Khon et al. 2010). Future development in the Arctic, including increased extraction of mineral and petroleum resources as well as expanded tourism and community development, will further increase exposure of Arctic ports to ship traffic and the potential for ballast-mediated invasions (Arctic Council 2009). Such changes in shipping activities, in combination with climate warming, will increase the potential for successful ballast-mediated invasions. Therefore, ballast water risk assessments are clearly needed for the region.

Here, I develop a framework to assess relative invasion risk for a vector transporting an unknown species assemblage, using ballast water transport in the Canadian Arctic as a case study. The objectives of the study are two-fold: first, to characterize ballast water discharge patterns for different vessel pathways in the region and, second, to identify ports at relatively high risk of ballast-mediated invasions and the responsible vessel pathway. The principal goal of the study is to direct research and preventive management efforts at potentially high-risk sites and vessel pathways so that

Arctic ecosystems can be protected from the negative effects that often accompany biological invasions.

2.2 Methods and Materials

My relative risk assessment adopts methods from species-specific assessments (Orr 2003; Therriault and Herborg 2007), with modifications to accommodate the suite of unidentified NIS potentially associated with the ballast water vector. First, the probability of introduction was estimated by combining the individual probabilities of successful arrival as well as survival and establishment, based on ballast water discharge data and environmental similarity between source and recipient ports. Second, the potential magnitude of consequence of the introduction was estimated based upon the number of high-impact, ballast-mediated NIS recorded for ecoregions of source ports. Finally, the probability of introduction and the potential magnitude of consequence were combined for a relative invasion risk rating.

Estimating probability of arrival

A comprehensive database of ballast water discharges at Canadian Arctic ports between 2005 and 2008 was assembled using Transport Canada's Ballast Water Database (TCBWD; https://wwwapps2.tc.gc.ca/saf-sec-sur/4/cpscs-scepc/default.asp, accessed March 2009) as the primary data source. The Canadian Arctic, as defined by Transport Canada, covers all Canadian waters north of 60° and those in Ungava Bay, Hudson Bay, and James Bay (Figure 2.1). All vessels with a ballast capacity greater than eight m^3 are required to submit ballast water reports prior to their first port-of-call in Canadian waters.

I considered only merchant vessels for my study because other vessel types carry very little or no ballast water and do not consistently report ballast activities. Data self-reported by vessels to the TCBWD provides information on the ballast history for each vessel transit, including date, location, and volume of ballast uptake and discharge events, as well as any management activities. My database was then supplemented with shipping data from the Canadian Coast Guard's Information System on Marine Navigation (INNAV). Canada requires all commercial vessels to report to INNAV when crossing into each Traffic Service Zone, while additional voluntary reporting regularly occurs for the duration of the transit for safety reasons. Information reported to INNAV includes arrival and departure events as well as cargo and ballast operations at ports (in binary format; volumes are not reported), and all reports are date and time coded. I grouped vessels in the dataset into two pathways according to operation region: 'international' vessels that operated outside of the Canadian exclusive economic zone (EEZ) for at least part of the study period; and 'coastal domestic' vessels that transited outside the Canadian Arctic but operated exclusively within Canada's EEZ for the entire study period. There were no 'Arctic' vessels that operated exclusively within the Canadian Arctic for the entire study period.

Gaps in ballast water data existed for 26 coastal domestic vessels because vessels operating entirely within Canadian waters are not required to submit ballast water reports. Through industry contacts, I recovered ballast records for six of the 26 vessels. Remaining data gaps for 20 vessels, representing 639 of 1,161 total merchant transits, were filled in using cargo information in the INNAV database. Based on the established relationship between cargo and ballast water operations in commercial vessels (Rup et al.

2010; David et al. 2012), I assumed that vessels discharged ballast water if cargo was loaded, resulting in 77 transits with ballast water discharge. Consultation with the shipping industry confirmed low frequency of ballast water discharges by vessels transporting supplies to northern communities (i.e. annual sealift); since the vessels were generally fully laden with cargo, they carried very little or no ballast water during transits to Arctic ports. I estimated discharge volumes for 50 of these transits using the historical median discharge volume previously reported by the same vessel on non-Arctic transits, since Rup et al. (2010) demonstrated that a single vessel carries a typical volume of ballast water on 90% of domestic transits. Discharge volumes for the remaining 27 transits by vessels without prior history were estimated using data for vessels of similar type and size class, since 'sister ships' typically carry similar volumes of ballast water (Rup et al. 2010). Analysis of ballast water reports submitted by international and coastal domestic vessels indicated that 80% of vessels loaded ballast at the last port-of-call, therefore I assigned the last port-of-call as the source of ballast water when ballast water history was incomplete. Further, I concluded that ballast was moved directly between domestic ports since domestic voyages are exempt from management regulations.

Ballast water exchange is documented as 90% effective for saline source water and 99% effective for freshwater sources, respectively (Ruiz and Smith 2005; Gray et al. 2007). Thus, the volume of ballast water discharged by vessels conducting ballast water exchange was corrected to account for the reduction in propagule pressure, using correction factors of 0.1 or 0.01 for vessels with ballast water from saline or freshwater source ports, respectively. For instance, a ship with reported discharge volume of 10,000 m^3 of ballast water, of which 6,000 m^3 originated from a saline source port and 4,000 m^3

from a freshwater source port, would be corrected using both correction factors resulting in 640 m^3 of ballast water being evaluated.

To characterize ballast water discharge patterns in the region, I summarized the geographic source location of ballast water by region, including the Arctic, Northwest Atlantic, Northeast Atlantic, West-central Atlantic, East-central Atlantic, Southeast Atlantic, and Mediterranean and Black Seas, as described by the Food and Agriculture Organization (FAO 2009) and as used in previous ballast water studies (see Simard and Hardy 2004; Claudi and Ravishankar 2006). Analysis of variance (ANOVA) was conducted to examine differences in annual discharge volume from different source regions in SPSS version 19.0 (IMB Corp. 2010). In addition, corrected ballast water discharge volumes were organized by month of discharge and operation region. In the absence of direct biological measures from ballast tanks, the corrected volume of ballast water discharged was used as a proxy for the propagule supply of NIS potentially arriving at ports (Rup et al. 2010; Lo et al. 2012). A ranking system was used to convert volume of ballast water discharged into a relative probability of arrival, where the maximum mean annual corrected volume of ballast water discharged at any single Arctic port was divided into five equal categories (Table 2.1). I used a positive linear relationship between the two variables consistent with the linear multi-species models in previous ballast water studies (Ricciardi 2001, 2006; Drake and Lodge 2004; Reusser 2010). Owing to the large number of ports in the region, I prioritized the top three ports in each vessel category, based on the probability of arrival, for further assessment.

Estimating probability of survival and establishment

All ports directly connected as a ballast water source to each top Arctic port were noted, allowing identification of source-recipient port-pairs. A comparison of environmental similarity between port-pairs was conducted to estimate relative probability of survival and establishment for all possible species that may be released into the new environment by ballast water (Gollasch 2002a; Clarke et al. 2004; Barry et al. 2008). I focused my analysis on temperature and salinity because they are fundamental factors affecting survival and reproduction of virtually all aquatic life (Anger 1991; Browne and Wanigasekera 2000). In addition, including variables that are related to invasion risk for only a subset of all potential NIS can dramatically influence the sensitivity of the environmental similarity measure (Barry et al. 2008). Following Keller et al. (2011), I selected four parameters to estimate environmental similarity between port-pairs, including annual mean water temperature, mean water temperature during the warmest month, mean water temperature during the coldest month, and annual mean salinity. Mean temperature provides a good indication of broad climatic zone, while maximum and minimum temperatures relate to upper and lower thermal limits of species (Angilletta 2009). A single salinity variable was used because it was the only salinity data available for most ports at a global scale (Keller et al. 2011). Data for the four parameters were obtained from Keller et al. (2011) for 6,651 ports worldwide. In addition, I interpolated environmental data in ArcGIS 10.1 (ESRI 2012) for 56 Arctic ports not included in Keller et al. (2011) using data from the World Ocean Atlas (Antonov et al. 2006; Locarnini et al. 2006). All environmental variables were standardized using a z-transformation to remove scale differences (Clarke et al. 2004; Keller et al. 2011).

I calculated the environmental similarity between port-pairs using Euclidean distance in four-dimensional space (Clarke et al. 2004; Barry et al. 2008; Keller et al. 2011). Additionally, I conducted a linear regression and sensitivity analysis to determine the relative importance of each parameter in the environmental similarity calculations (see Keller et al. 2011). While salinity was found to have equal weighting as the three temperature variables combined in a study on the Great Lakes (Keller et al. 2011), environmental similarity between top Arctic ports and global ports is driven by mean temperature during the warmest month and mean temperature during the coldest month. While I could reduce the number of temperature variables to redistribute the influence of salinity in the environmental similarity calculations, I suggest that including all three temperature parameters is appropriate for this study because temperature range rather than salinity distinguishes top Arctic ports from other global ports. Similarly, a review by Chown et al. (2010) suggested that thermal extremes were more important than mean environmental temperature in determining species performance. Furthermore, I found that using different numbers and combinations of environmental variables in the environmental similarity calculation altered some risk ratings for individual port-pairs but did not change final invasion risk estimates.

Environmental distance values between each top port and all connected source ports were averaged to obtain a final rating for survival and establishment potential. A ranking system was used to convert the average environmental distance value for each port into a relative probability of survival and establishment, where the maximum value for any single source-recipient port-pair (of all possible global port-pairs, not just those that were connected in this dataset) was divided into five equal categories (Table 2.1).

The choice of five equal categories reflects a positive linear correlation between the likelihood of NIS survival and establishment and the degree of environmental similarity between donor and recipient ports, an assumption that has been used in previous environmental matching studies (e.g. Hilliard et al. 1997; Hewitt and Hayes 2002; Clarke et al. 2004). I conducted the environmental similarity analysis on all possible global ports so that the ranking system would cover the full range of environmentally similar and dissimilar values (Clarke et al. 2004).

Calculating probability of introduction

Probabilities of arrival as well as survival and establishment were combined into a probability of introduction using Orr's (2003) minimum probability method. For example, a 'higher' probability of arrival combined with a 'lower' probability of survival and establishment would result in 'lower' probability of introduction. Because the outcome of each individual invasion stage is independent, but successful transition through all stages is a prerequisite for introduction, the probability of passing through all invasion stages would be equal to or lower than the probability of any individual stage (Orr 2003).

Estimating magnitude of potential consequence

I compiled a list of high-impact, ballast-mediated NIS for connected source ports using data from the Nature Conservancy's Marine Invasive Database (Molnar et al. 2008) because current, port-specific lists of native species and established NIS are not available globally. Molnar et al. (2008) quantifies NIS impact using a semi-quantitative ecological

impact scoring system. The score was assigned globally for each species, reflecting the most damaging documented impact on the viability and integrity of native species and biodiversity (Molar et al. 2008). Under this scoring system, all high-impact NIS considered in the risk assessment have received a score of at least three in the four-point system, and disrupt multiple species, ecosystem function, and/or keystone or threatened species. The database includes 90 high-impact, ballast-mediated NIS in 232 ecoregions. I tabulated the number of high-impact NIS recorded for the ecoregion of each connected source port assuming that each port may be a donor of all high-impact NIS established within the ecoregion; therefore, multiple tally counts were given to a single NIS that could originate from multiple source ports within an ecoregion. For example, a top port connected to three different ecoregions via four source ports (two source ports being located within one ecoregion) with 10 high-impact NIS recorded in each ecoregion would result in a cumulative total of 40 high-impact NIS. A NIS originating from multiple source populations were tallied multiple times because the introduction of different genotypes of a single species can increase impact in the recipient environment through increased genetic variation and evolutionary potential (Sakai et al. 2001).

A ranking system was used to convert the cumulative number of high-impact NIS connected to each top Arctic port into a relative magnitude of potential consequence, where the maximum value was divided into five equal categories (Table 2.1). I used a linear relationship between the two variables for two reasons. First, all high-impact NIS considered have strong and roughly equal magnitude of consequences globally according to the ecological impact score system provided by Molnar et al. (2008). Therefore, a given increase in number of high-impact NIS should lead to a proportional increase in the

magnitude of potential consequence. Second, the linear impact model of Parker et al. (1999) describes impact as a function of abundance and effect per individual of a particular species; in this case, potential impact is a function of the number of potential high-impact NIS and effect per species.

Calculating invasion risk

The probability of introduction and magnitude of potential consequences of ballast-mediated NIS were combined into a final relative invasion risk rating using a symmetrical mixed-rounding matrix that reduces the final ratings to three levels (modified from Therriault and Herborg 2007; Table 2.2).

2.3 Results

During the study period, 29 Arctic ports received an annual mean ballast water discharge of 275,714 (± 6,644) m^3, or 92,625 (± 11,251) m^3 after correcting for reduction in propagule supply following ballast water exchange (Table 2.3). The number of discharge events decreased over time, though a similar volume was reported each year. Ninety-five percent of ballast water discharges took place between July and November, with peak discharge in August. The annual total corrected volume discharged differed significantly by source region (ANOVA, $p < 0.05$), with most water originating from Canadian ports in the Arctic (29,770 ± 9,852 m^3) and Northwest Atlantic (25,693 ± 11,344 m^3), followed by unknown sources (12,345 ± 5,318 m^3) and foreign ports in Northeast Atlantic (8,697 ± 2,166 m^3), Mediterranean and Black Seas (2,185 ± 678 m^3), West-central Atlantic (878 ± 608 m^3), East-central Atlantic (262 ± 262 m^3), and

Southeast Atlantic (234 ± 234 m^3). Ballast water discharge patterns varied spatially, with ports in Hudson Bay receiving the greatest corrected volume of ballast water (76,145 ± 9,757 m^3), followed by those in the Eastern Arctic (16,308 ± 5,057 m^3) and Western Arctic (173 ± 173 m^3) (Figure 2.1).

Twenty-seven (± 1.7) international merchant vessels discharged an annual mean of 197,589 (± 15,271) m^3 of ballast water, or 70,097 (± 8,182) m^3 after correcting for reduction in propagule supply following ballast water exchange. Churchill (Manitoba), Milne Inlet (Nunavut), and Deception Bay (Québec) received the greatest total corrected volume of ballast water discharged by international merchant vessels (Table 2.4). However, only Churchill had 'highest' probability for ballast-mediated NIS arrival via international merchant vessel discharges. Arrival probabilities for the remaining top ports ranged from 'lowest' to 'lower'. On the other hand, 12 (± 2.0) coastal domestic merchant vessels discharged an annual mean of 78,125 (± 13,802) m^3, or 22,528 (± 3,947) m^3 corrected volume of ballast water. Churchill, Deception Bay, and Iqaluit (Nunavut) received the greatest total corrected volume of ballast water discharged by coastal domestic merchant vessels (Table 2.4). The probability of arrival of ballast-mediated NIS via coastal domestic merchant vessel discharges was 'lowest' for all top Arctic ports.

Forty-eight foreign, two coastal domestic, and one Arctic source ports were connected to Churchill by international merchant vessels, with an 'intermediate' overall probability of survival and establishment; 29 source ports had 'higher' or 'highest' environmental similarity with Churchill (Supplementary Table S2.1). One coastal domestic source port was connected to Milne Inlet by international merchant vessels, with an 'intermediate' probability of survival and establishment (Supplementary Table

S2.1). Similarly, one foreign, two coastal domestic, and one Arctic source ports were connected to Deception Bay by international merchant vessels, with a 'higher' overall probability of survival and establishment; four source ports had 'higher' or 'highest' environmental similarity with Deception Bay (Supplementary Table S2.1). One coastal domestic and five Arctic source ports were connected to Churchill by coastal domestic merchant vessels, with a 'highest' overall probability of survival and establishment; all of these source ports had 'highest' environmental similarity with Churchill (Supplementary Table S2.2). Five coastal domestic source ports were connected to Deception Bay by coastal domestic merchant vessels, with an 'intermediate' overall probability of survival and establishment; one source port had 'highest' environmental similarity with Deception Bay (Supplementary Table 2.2). Similarly, two Arctic source ports were connected to Iqaluit by coastal domestic vessels, with a 'highest' overall probability of survival and establishment; all source ports had 'highest' environmental similarity with Iqaluit (Supplementary Table S2.2).

Based on the probabilities of arrival as well as survival and establishment, all top ports have a 'lowest' to 'intermediate' probability of introduction of ballast-mediated NIS (Table 2.5). The cumulative number of high-impact, ballast-mediated NIS at each top port by vessel category ranged from one to 875, representing 78 distinct NIS (Table 2.1 and Supplementary Table S2.3). Churchill was rated 'highest' for magnitude of potential consequence of NIS introduction via international merchant vessel discharges, while the remaining top ports rated 'lowest' for magnitude of potential consequence (Table 2.5). The final relative invasion risk based on a combination of probability of introduction and magnitude of potential consequence indicated that Churchill has 'higher' risk for ballast-

mediated invasions via international merchant ballast water discharges than any other recipient port studied (Table 2.5). The invasion risk for the remaining top ports was 'lower'.

2.4 Discussion

Using a relative risk assessment framework based on the estimated probability that potential NIS will successfully arrive, survive and establish, as well as the magnitude of potential consequence, Churchill appears to be at greatest invasion risk from discharge of ballast water by international merchant vessels despite requirements for ballast water exchange for incoming foreign transits. The estimated invasion risk is driven mainly by Churchill's high connectivity to a variety of foreign ports, and a high magnitude of potential impact in consequence. Churchill is a major Arctic seaport for grain export owing to its proximity to the Canadian prairies and its connection to the rail transit system, thus it attracts numerous international merchant vessels that discharge both domestic and foreign ballast water (McCalla 1994; Niimi 2007). All other ports assessed resulted in a lower invasion risk due to a low probability of NIS arrival and/or low magnitude of potential consequence.

Ballast water from coastal domestic sources in the Arctic and Northwest Atlantic appear to pose a relatively high risk of introducing new NIS or spreading established ones, representing 85% of total corrected volume of ballast water discharged at Canadian Arctic ports. The majority of this volume was not exchanged because ballast water originating from domestic sources is presently exempt from ballast water management regulations. Moreover, domestic voyages are generally shorter and associated with higher density of viable organisms in ballast water discharges (Simkanin et al. 2009; Lawrence

and Cordell 2010; DiBacco et al. 2012). On the other hand, ballast water from foreign sources must be exchanged or flushed on the open ocean, which dramatically reduces potential propagule pressure to Canadian ports. It is important to note that international merchant vessels carried ballast water from both domestic and foreign sources and appear to be the main vessel category delivering domestic ballast water and potentially NIS into the region.

The observed temporal and spatial patterns of ballast water discharge suggest that potential invasion risk is not uniform in the Canadian Arctic. Not surprisingly, ballast water discharges took place mainly during summer months, coinciding with high abundance of food and favourable environmental conditions for many species in the Arctic. The timing of propagule arrival may allow NIS to reproduce and form established populations or produce diapausing eggs before environmental conditions deteriorate, thus increasing the probability of successful colonization (Crawley 1989; Bailey et al. 2009). Additionally, discharges were concentrated in Hudson Bay, where climatic conditions are relatively mild and more similar to those of temperate regions, enhancing the probability of survival of released NIS. Therefore, ports in Hudson Bay may be at highest ballast-mediated invasion risk during summer months.

From a global perspective, the Canadian Arctic currently receives less vessel traffic and a smaller volume of ballast water discharge than most temperate regions. For example, the volume of ballast discharged in the region is 0.4% of that in the Great Lakes and St. Lawrence River (Bailey et al. 2011) and 1% of that on the west coast of the United States (Simkanin et al. 2009). The Canadian Arctic also has less vessel traffic than other Arctic regions, with approximately 10% of the number of vessel arrivals to Alaska

(McGee et al. 2006; Arctic Council 2009). It is important to note, however, that the short season and condensed spatial pattern of propagule arrival in the Canadian Arctic may negatively bias comparisons of annual averages. In addition, marine shipping in the Arctic is expected to grow in the near future coincident with sea ice retreat. Increased resource exploration, tourism, and research are expected to be major contributors to shipping growth in the Arctic (Arctic Council 2009). Current environmental conditions of some Arctic and sub-Arctic regions can be suitable for temperate species, thus successful establishment is possible given adequate propagule supply (de Rivera et al. 2011). In fact, at least 10 NIS have been reported in Arctic and sub-Arctic waters, although the mechanism(s) of introduction and confirmation of long-term establishment success is generally not well documented (Hines and Ruiz 2000; Streftaris et al. 2005; Gollasch 2006; Molnar et al. 2008). The small number of NIS recorded in the Arctic may be an artifact of insufficient research effort (Niimi 2004; Ruiz and Hewitt 2009).

The Arctic remains a relatively pristine ecosystem (Arctic Council 2009). Precautionary preventive management efforts may protect Canadian and other Arctic ecosystems from biological invasions, especially at relatively high-risk ports. My results also suggest that vector management polices should include domestic ballast water carried by international merchant vessels. In addition, biological surveys can be directed at high-risk sites to gather information on the quantity and diversity of potential NIS associated with the vector and/or to fill data gaps. This framework can be used to monitor changes in invasion risk in the Canadian Arctic as the region experiences climate warming and increased shipping activity.

Several limitations of my relative risk assessment warrant discussion. First, my estimate of ballast water discharged by coastal domestic vessels into the region was largely based on the assumption that ballast water was discharged when cargo was loaded. This approach may over- or under-estimate actual volume discharged depending on the quantity of the cargo loaded in relation to the vessels' deadweight (David et al. 2012). In the absence of ballast information for this subset of vessels, my approach utilized best available data and was informed by government agencies and the shipping industry. Second, I used volume of ballast water discharged as a proxy measure for the biota actually released at ports. This relationship may not be robust in certain cases, with propagule supply more strongly associated with water salinity, age of ballast water, and management practices (Verling et al. 2005; Lawrence and Cordell 2010). While my methods did account for ballast water exchange, I was unable to incorporate additional factors affecting propagule supply. The use of ballast volume as a proxy for propagule pressure, while imperfect, is consistent with a number of previous studies (Drake and Lodge 2004; Herborg et al. 2007; Simkanin et al 2009; Lo et al. 2012).

Third, the environmental similarity analysis may under- or over- estimate NIS survival and establishment risk for individual species because biological interactions, such as facilitation, competition and predation, which can have positive or negative impacts on NIS in the new environment, were not evaluated (Barry et al. 2008). While I recognize these limitations, my approach follows established assumptions and recommendations of previous environmental similarity analyses using the most comprehensive global port environmental data (e.g. Hewitt and Hayes 2002; Clarke et al. 2004; Barry et al. 2008; Keller et al. 2011). Finally, the list of high-impact NIS used to

estimate magnitude of potential consequence was available only for ecoregions rather than specific ports. It does not account for species that may cause high impacts in new recipient regions despite low or negligible impact in source regions, and it does not account for high-impact species that are native to the source region. Additionally, the approach assumes that the effect per high-impact NIS is independent of other species. Although NIS impacts are known to vary depending on the physical and biological characteristics of the invaded environment, I was not able to evaluate these factors due to limited port-specific NIS records. While not ideal, this data is peer-reviewed and is the most comprehensive global NIS data available.

All risk assessments have an inherent level of uncertainty since they are an estimate of a complex biological process and can never capture all variables involved (Orr 2003). In fact, risk assessments are most needed when knowledge regarding individual NIS or vectors is limited, or most uncertain. The uncertainty associated with my vector-based relative risk assessment is mainly related to the quality of data (i.e. degree of error) available and the representativeness of the data in terms of the invasion process (i.e. degree of mismatch). The degree of error in my relative assessment is generally low because all data used were obtained from extensive systematic information or peer-reviewed data. The degree of mismatch is low to moderate because the relationship between invasion success and the proxy measures used to estimate probabilities of arrival, survival and establishment, and consequence were based on substantial scientific information and peer-reviewed literatures. The National Research Council (2011) provided an extensive theoretical treatment of the risk-release relationship, surmising that the combined curves of multiple populations would be expected to be non-linear but

might be better characterized as linear due to other important sources of variation that affect invasion probability. Thus, I chose a linear model for my relative ranking system, which is consistent with previous ballast water studies (e.g. Ricciardi 2001, 2006; Drake and Lodge 2004; Reusser 2010). I acknowledge that additional research to improve the degree of mismatch would benefit future vector-based risk assessments.

To my knowledge, this is the most comprehensive vector-based relative risk assessment for assessing potential invasions where the identity of NIS associated with the vector is unknown. By evaluating all stages of the invasion process and the magnitude of potential consequence, I estimated the relative invasion risk at major ports and identified risky transit pathways for the Canadian Arctic. The framework presented here could be applied to other mechanisms of biological invasion where the vast number of potential NIS within a vector prohibits species-specific assessment. The information needed will vary according to vector but should include a measure of vector strength such as the number of arrivals, identification of source and release sites of potential NIS (i.e. the pathway), environmental conditions at those sites, as well as a means to measure potential consequence. By following these steps and adopting a risk ranking system, one can estimate the relative probability of introduction and potential magnitude of consequence for NIS within a vector at a variety of locations or across different geographic pathways.

Table 2.1 Ranking system for probabilities of arrival as well as survival and establishment, and magnitude of consequence of nonindigenous species (NIS) at Canadian Arctic ports.

Mean annual corrected volume of ballast water discharged (m^3)	**Environmental distance**	**Cumulative number of high-impact NIS**	**Risk rating**
27,734 – 34,667	0.00 – 1.40	701 – 875	Highest
20,801 – 27,733	1.41 – 2.80	526 – 700	Higher
13,867 – 20,800	2.81 – 4.20	351 – 525	Intermediate
6,934 – 13,866	4.21 – 5.60	176 – 350	Lower
0 – 6,933	4.61 – 7.00	0 – 175	Lowest

Table 2.2 Matrix used to combine probability of introduction and magnitude of consequence of introduction into final risk ratings, modified from Therriault and Herborg (2007); stippled = lower risk, grey = intermediated risk, black = higher risk.

		P (Introduction)				
		Lowest	Lower	Intermediate	Higher	Highest
Consequence	Highest					
	Higher					
	Intermediate					
	Lower					
	Lowest					

Table 2.3. Annual discharge statistics at Canadian Artic ports, by ballast water source. Correction factors (10% for saline and 1% for freshwater source ports, respectively) were applied to account for reduction in propagule supply due to ballast water exchange. 'Direct' refers to water that was not managed prior to discharge.

Year	Discharge events	Volume of ballast water discharge (m^3)								
		Grand Total	Corrected foreign exchanged		Corrected coastal domestic exchanged		Coastal domestic direct	Arctic direct	Unknown source	Corrected Total
			10%	1%	10%	1%				
2005	44	259,623	7,934	34	69	641	46,282	55,044	10,802	120,805
2006	41	291,652	15,402	0	1,025	513	0	50,190	25,927	93,057
2007	36	272,890	18,489	27	1,973	205	9,297	24,375	11,397	65,763
2008	35	278,690	11,846	0	0	820	38,548	39,663	0	90,877
Mean	39	275,714	13,418	15	767	545	23,532	42,318	12,032	92,625
(±S.E.M.)	(2)	(6,644)	(2,277)	(9)	(465)	(130)	(11,178)	(6,788)	(5,321)	(11,251)

Table 2.4 Ballast water discharge statistics for international merchant and coastal domestic vessels at the top five Arctic ports. Asterisks denote the top three ports considered for full assessment in each vessel category.

Top 5 ports	No. of discharge events	Mean (± S.E.M.) annual volume of ballast water discharge (m^3)		
		Grand Total	Corrected Total	P (Arrival)
International merchant vessel ballast water discharges				
Churchill, MB*	17 (2)	157,675 (19,409)	34,667 (8,661)	Highest
Milne Inlet, NU*	0.3 (0.3)	6,959 (6,959)	6,959 (6,959)	Lower
Deception Bay, QC*	1.5 (0.3)	8,069 (4,020)	3,884 (2,073)	Lowest
Iqaluit, NU	1.3 (0.3)	3,679 (1,548)	3,679 (1,548)	Lowest
Aupaluk, QC	0.8 (0.3)	3,236 (1,105)	3,236 (1,105)	Lowest
Coastal domestic merchant vessel ballast water discharges				
Churchill, MB*	2 (1.4)	5,221 (3,319)	5,221 (3,319)	Lowest
Deception Bay, QC*	6 (1.2)	60,144 (11,852)	4,457 (2,102)	Lowest
Iqaluit, NU*	0.5 (0.3)	1,536 (896)	1,536 (896)	Lowest
Chesterfield Inlet/Igjugarjuk, NU	0.3 (0.3)	1,468 (1,468)	1,468 (1,468)	Lowest
Nanisivik, QC	0.3 (0.3)	1,468 (1,468)	1,468 (1,468)	Lowest

Table 2.5 Relative invasion risk for ballast-mediated introductions at top Arctic ports by vessel category. NIS = nonindigenous species.

	P(Arrival)	P(Survival and Establishment)	P(Introduction)	Cumulative no. of high-impact NIS	Magnitude of potential consequence	Invasion risk
International merchant vessel ballast water discharges						
Churchill, MB	Highest	Intermediate	Intermediate	875	Highest	Higher
Milne Inlet, NU	Lower	Intermediate	Lower	3	Lowest	Lower
Deception Bay, QC	Lowest	Higher	Lowest	47	Lowest	Lower
Coastal domestic merchant vessel ballast water discharges						
Churchill, MB	Lowest	Highest	Lowest	8	Lowest	Lower
Deception Bay, QC	Lowest	Intermediate	Lowest	12	Lowest	Lower
Iqaluit, NU	Lowest	Highest	Lowest	1	Lowest	Lower

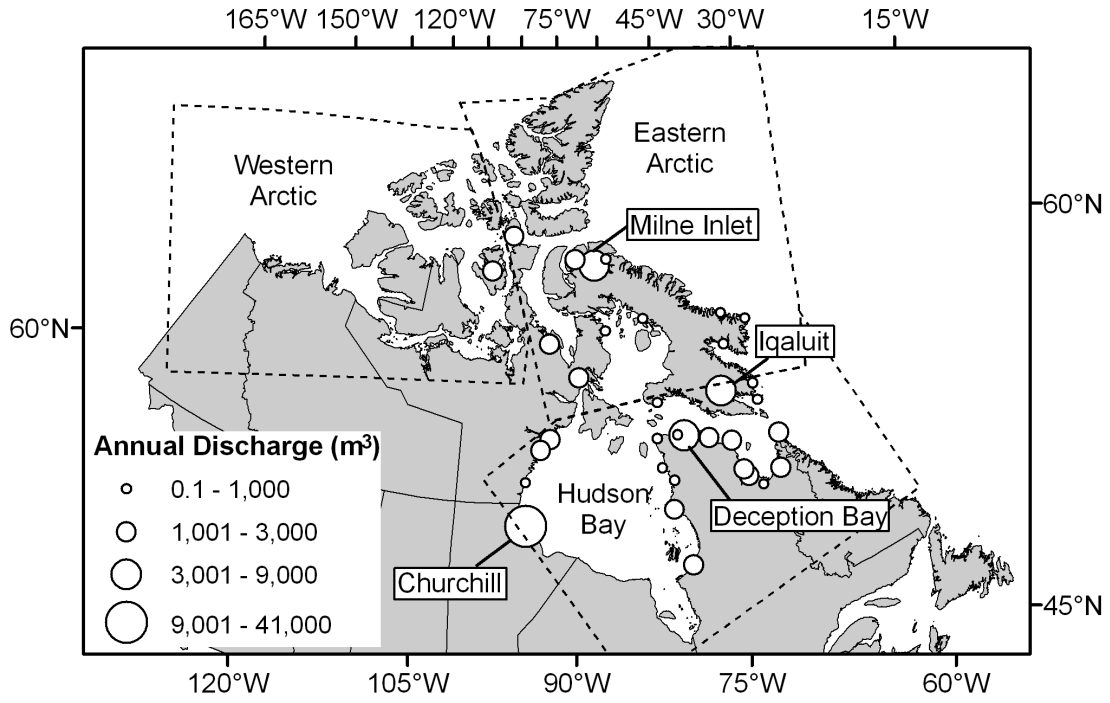

Figure 2.1. Map illustrating the spatial distribution of corrected ballast water discharges in the Canadian Arctic by region: Hudson Bay, Eastern Arctic, and Western Arctic. Dotted-line polygons outline the boundaries of the Arctic regions, following Canadian Ice Services (2009). Top ports selected for full risk assessment are labeled.

2.5 Supplementary Information

Table S2.1. Environmental distance between top and source ports connected via ballast water discharge by international merchant vessels. Asterisks denote source ports that received higher or highest probability of survival.

Source port	Source port country	Environmental distance	P(Survival)
Churchill-			
Algiers	Algeria	3.59	Intermediate
Amsterdam*	Netherlands	2.32	Higher
Annaba	Algeria	3.64	Intermediate
Antwerp	Belgium	2.84	Intermediate
Aughinish*	Ireland	2.27	Higher
Aupaluk	Canada	1.26	Highest
Aviles*	Spain	2.75	Higher
Baltimore	United States	3.53	Intermediate
Belfast*	United Kingdom	1.68	Higher
Bremen*	Germany	1.95	Higher
Cartagena	Spain	3.64	Intermediate
Casablanca	Morocco	3.46	Intermediate
Ceyhan	Turkey	4.02	Intermediate
Charleston	United States	3.97	Intermediate
Civitavecchia	Italy	3.43	Intermediate
Dublin*	Ireland	1.47	Higher
Foynes*	Ireland	2.23	Higher
Gdynia*	Poland	2.10	Higher
Ghent*	Belgium	2.79	Higher
Gibraltar	Gibraltar	3.09	Intermediate
Gijon*	Spain	2.74	Higher
Greenore*	Ireland	1.53	Higher
Hamburg*	Germany	1.91	Higher
Houston	United States	4.54	Lower
Ijmuiden*	Netherlands	2.00	Higher
Klaipeda*	Lithuania	2.32	Higher
Liepaja*	Latvia	2.20	Higher
London*	United Kingdom	2.74	Higher
Londonderry*	United Kingdom	1.87	Higher
Lorient*	France	2.42	Higher
Malaga	Spain	3.63	Intermediate
Matadi	Congo	4.94	Lower
Newport*	United Kingdom	2.19	Higher
Newport News	United States	3.44	Intermediate
Oran	Algeria	3.80	Intermediate

Port Alfred*	Canada	1.84	Higher
Port Everglades	United States	5.10	Lower
Portbury*	United Kingdom	2.03	Higher
Québec	Canada	2.90	Intermediate
Ravenna	Italy	3.23	Intermediate
Riga*	Latvia	2.36	Higher
Rönnskär*	Sweden	1.86	Higher
Rotterdam*	Netherlands	2.70	Higher
Santiago	Cuba	4.88	Lower
Savannah	United States	4.24	Lower
Straumsvik*	Iceland	0.94	Highest
Sunndalsøra*	Norway	1.97	Higher
Tampa*	United States	4.68	Lower
Tarragona	Spain	3.47	Intermediate
Teesport*	United Kingdom	1.51	Higher
Terneuzen*	Netherlands	2.29	Higher
Overall		**2.83**	**Intermediate**
Milne Inlet-			
Port Alfred	Canada	2.94	Intermediate
Overall		**2.94**	**Intermediate**
Deception Bay-			
Aarhus	Denmark	2.81	Intermediate
Belledune*	Canada	2.09	Higher
Rankin Inlet*	Canada	1.16	Highest
Saint John*	Canada	2.75	Higher
Overall		**2.20**	**Higher**

Table S2.2. Environmental distance between top and source ports connected via ballast water discharge by coastal domestic merchant vessels. Asterisks denote source ports that received higher or highest probability of survival.

Source port	Source port country	Environmental distance	P(Survival)
Churchill-			
Arviat*	Canada	0.51	Highest
Baker Lake*	Canada	0.75	Highest
Igloolik*	Canada	1.30	Highest
Rankin Inlet*	Canada	0.48	Highest
Repulse Bay*	Canada	1.18	Highest
Sept Iles*	Canada	1.03	Highest
Overall		**0.87**	**Highest**
Deception Bay-			
Bécancour	Canada	3.87	Intermediate
Chicoutimi	Canada	3.74	Intermediate
Montréal	Canada	4.11	Intermediate
Québec	Canada	3.86	Intermediate
Voisey's Bay*	Canada	0.27	Highest
Overall		**3.17**	**Intermediate**
Iqaluit-			
Kangiqsujuaq*	Canada	0.91	Highest
Killinek*	Canada	1.03	Highest
Overall		**0.97**	**Highest**

Table S2.3. High-impact, ballast-mediated NIS established at ports directly connected to top Arctic ports.

Species	Higher taxa	Top ports			
		Churchill	Deception Bay	Iqaluit	Milne Inlet
Acartia tonsa	Crustacean	x	x		
Acrothamnion preissii	Plant	x			
Aglaothamnion halliae	Algae	x	x		
Alepes djedaba	Fish	x			
Alexandrium catenella	Algae	x			
Alexandrium minutum	Algae	x			
Alexandrium ostenfeldii	Algae	x	x		x
Alexandrium peruvianum	Algae	x			
Alexandrium taylori	Algae	x			
Anadara inaequivalvis	Mollusc	x			
Asparagopsis armata	Plant	x			
Balanus improvisus	Crustacean	x			
Botryllus schlosseri	Tunicate	x	x		
Botryllus violaceus	Tunicate	x	x		
Brachidontes pharaonis	Mollusc	x			
Callinectes sapidus	Crustacean	x	x		
Carcinus maenas	Crustacean	x	x		
Caulerpa racemosa var. *cylindracea*	Plant	x			
Caulerpa taxifolia	Plant	x			
Cercopagis pengoi	Crustacean	x	x		
Chara connivens	Algae	x	x		
Charybdis hellerii	Crustacean	x			
Chattonella aff. *verruculosa*	Algae	x	x		
Codium webbiana	Algae	x	x		
Corbula gibba	Mollusc	x	x		
Cordylophora caspia	Cnidarian	x	x		
Coscinodiscus wailesii	Diatom	x	x		
Crepidula fornicata	Mollusc	x	x		
Dasya baillouviana	Algae	x	x		
Didemnum cf. *lahillei*	Ascidian	x	x		
Dreissena polymorpha	Mollusc	x	x	x	x
Dyspanopeus sayi	Crustacean	x			
Elminius modestus	Crustacean	x	x		
Eriocheir sinensis	Crustacean	x	x		
Ficopomatus enigmaticus	Annelid	x	x		
Gammarus tigrinus	Crustacean	x	x		
Garveia franciscana	Cnidarian	x			
Hemigrapsus penicillatus	Crustacean	x			

Hemigrapsus sanguineus	Crustacean	x	x		
Hemimysis anomala	Crustacean	x			
Heterosiphonia japonica	Algae	x	x		
Hydroides ezoensis	Annelid	x	x		
Lithoglyphus naticoides	Mollusc	x			
Littorina littorea	Mollusc	x	x		
Lophocladia lallemandii	Algae	x			
Maeotias marginata	Cnidarian	x	x		
Marenzelleria neglecta	Annelid	x	x		
Marenzelleria viridis	Annelid	x	x		
Membranipora membranacea	Bryozoan	x	x		
Moerisia lyonsi	Cnidarian	x			
Musculista senhousia	Mollusc	x			
Mya arenaria	Mollusc	x	x		
Mytella charruana	Mollusc	x			
Mytilopsis leucophaeata	Mollusc	x			
Neogobius melanostomus	Fish	x			
Ostreopsis ovata	Algae	x			
Percnon gibbesi	Crustacean	x			
Perna perna	Mollusc	x			
Perna viridis	Mollusc	x			
Phyllorhiza punctata	Cnidarian	x			
Polyandrocarpa zorritensis	Tunicate	x			
Polydora ciliata	Annelid	x	x		
Polydora cornuta	Annelid	x			
Polysiphonia morrowii	Algae	x			
Pontogammarus robustoides	Crustacean	x			
Prorocentrum minimum	Diatom	x	x		
Pseudobacciger harengulae	Annelid	x	x		
Pseudopolydora paucibranchiata	Annelid	x			
Rapana venosa	Mollusc	x			
Rhithropanopeus harrisii	Crustacean	x	x		
Rhopilema nomadica	Cnidarian	x			
Sargassum muticum	Algae	x	x		
Spartina anglica	Plant	x	x		
Strombus persicus	Mollusc	x			
Styela clava	Tunicate	x	x		x
Theora lubrica	Mollusc	x			
Undaria pinnatifida	Plant	x	x		
Xenostrobus securis	Mollusc	x			

CHAPTER 3: COLONIZATION PRESSURE – TOTAL PROPAGULE PRESSURE RELATIONSHIPS FOR INVERTEBRATES IN BALLAST WATER: TEMPERATE VERSUS ARCTIC COMPARISONS[2]

3.1 Introduction

The invasion process can be viewed as a series of stages including arrival, survival, establishment, and spread, where successful transition to subsequent stages is determined by a number of factors including the number of arriving species and their abundance (i.e. colonization pressure [CP] and propagule pressure [PP]), physico-chemical factors, and community interactions (Kolar and Lodge 2001; Colautti et al. 2006; Lockwood et al. 2007; Blackburn et al. 2011). Despite the complex nature of the invasion process and the number of factors that influence it, CP and PP remain important null models for biological invasions (Colautti et al. 2006; Lockwood et al. 2009). Increasing the number of introduction events or the number of propagules released per event enhances the probability of establishment of a population due to decreased environmental and demographic stochasticity, respectively (Colautti et al. 2006; Lockwood et al. 2009; Simberloff et al. 2009). Similarly, a greater number of species introduced increases the potential that at least one species can form a self-sustaining population in the new environment (Lockwood et al. 2009), where matching environmental conditions between source and recipient habitats provides the greatest opportunity for establishment success (Herborg et al. 2007; Barry et al. 2008; Floerl et al. 2013). Therefore, a first step in

[2] Chan FT, Briski E, Bailey SA, MacIsaac HJ (2014) Richness-abundance relationships for zooplankton in ballast water: temperate versus Arctic comparisons. ICES Journal of Marine Science 71:1876-1884

assessing invasion risk of a transport vector – particularly those capable of transferring large species assemblages – is to determine the arrival potential of transported species by quantifying the number of individuals introduced per species and the number of species released per introduction event (e.g. Conn et al. 2010; Haska et al. 2012; Briski et al. 2013).

Understanding the link between CP and PP for species assemblages being translocated by a transport vector can further improve our ability to predict invasions by identifying conditions where high- and low-risk introduction events are expected (see Lockwood et al. 2009; Briski et al. 2012). A high-risk introduction event may be characterized by a large number of species each represented by many individuals, a large number of species each represented by few individuals, or by a few abundant species, although I expect the first scenario to represent the greatest invasion risk because of the high likelihood for establishment of multiple species in the new environment. In contrast, a low-risk introduction event may be characterized by a small number of species each represented by few individuals. The relationship between CP and PP will depend on the nature of the vector, the source community, and survival and reproductive strategies of entrained organisms (Lockwood et al. 2009; Briski et al. 2012, 2014). For example, Briski et al. (2012) reported that the relationship between CP and total PP (i.e. total number of individuals of all species) varied across and within taxonomic groups sampled from ballast water of ships.

Temperature change is regarded as a principal environmental factor affecting survival of organisms, including those in ballast water (Gollasch et al. 2000a; Klein et al. 2010; Seiden et al. 2011). Other factors that may also cause mortality in ballast tanks

include food limitation, predation, light and oxygen limitation, mechanical injury due to wave action, and chemical toxicity associated with tank coatings (Carlton 1985; Gollasch et al. 2000b; Wonham et al. 2001). Increasing ballast water age prolongs the interval that organisms are exposed to these stressors, and thus usually adversely affects the number of organisms that survive (Gollasch et al. 2000b; Verling et al. 2005; Cordell et al. 2009). The effects of these selective pressures on organism survival during transport could vary depending on the shipping route because of exposure to different environmental conditions (Briski et al. 2013). As a result, CP, total PP, and subsequently the relationship between CP and total PP associated with ballast water could vary depending on the shipping route (e.g. Arctic versus temperate voyages).

While ballast water is one of the best characterized vectors of aquatic nonindigenous species (NIS) globally, very few studies have assessed the magnitude of the transport vector in the Arctic (e.g. Niimi 2004; Chan et al. 2013; Ware et al. 2013), and none have conducted biological sampling to determine community assemblages being transported in northern Canada. Arctic shipping plays an important role in supporting Canada's northern communities by delivering supplies and transporting Arctic resources to domestic and international markets (McCalla 1994). However, shipping may also provide opportunities for species to disperse into or within the region. For example, the Pacific diatom *Neodenticula seminae* reappeared in the Labrador Sea in 1999, though it was absent since the Pleistocene (Reid et al. 2007). While evidence suggests that the diatom was likely carried by increased flows of Pacific water from the Bering Sea through the Arctic Ocean following recession of coastal ices sheets, the possibility of introduction via ballast water cannot be dismissed (Reid et al. 2007). At least 10 aquatic

NIS have been reported in other Arctic and sub-Arctic waters, although the introduction pathway(s) and long-term establishment success are generally not well documented (Hines and Ruiz 2000; Streftaris et al. 2005; Gollasch 2006). Such a small number of NIS documented for the Arctic may be an artefact of limited research effort (Niimi 2004; Ruiz and Hewitt 2009). Therefore, an examination of the biological composition of ballast water of ships entering Canadian Arctic waters is needed to evaluate the arrival potential by this vector.

In this study, I determine the arrival potential of invertebrates via ballast water in the Canadian Arctic by comparing CP, total PP, and the CP:total PP relationship for ships arriving at the Port of Churchill to those bound for ports on the Atlantic coast and in the Great Lakes. Hereafter I use the terms 'Arctic', 'Atlantic', and 'Great Lakes' to denote ships destined for Churchill, the Atlantic coast, and Great Lakes, respectively. I have two objectives: First, to quantify CP and total PP of invertebrates as well as the relationship between the two parameters in ballast water of Arctic, Atlantic, and Great Lakes ships; and second, to examine transit factors such as temperature change and ballast water age that may influence CP and total PP of invertebrates, and subsequently the relationship between the two, in ballast water for different vessel groups. I quantify total abundance of all invertebrate species (i.e. total PP of all species) rather than abundance per species (i.e. PP) to be consistent with a number of previous ballast water studies (e.g. Lawrence and Cordell 2010; Verling et al. 2010; DiBacco et al. 2012) and to be consistent with the D-2 Ballast Water Performance Standard proposed by the International Maritime Organization, which sets a maximum allowable discharge concentration based on the total number of organisms, including invertebrates, per cubic metre of water (IMO 2004).

In addition, because of a major lack of baseline biodiversity information available for Canadian Arctic coastal ecosystems (see Cusson et al. 2007; Archambault et al. 2010), I could not confidently assign invasion status to invertebrate species collected from Arctic ships. The distinction between NIS and native species would also vary depending on the ballast water discharge location (see Briski et al. 2012). As a result, I did not differentiate NIS from native species when determining CP and total PP of invertebrates, and thus my results may be conservative estimates of invasion risk for invertebrates in ballast water.

3.2 Methods and Materials

Study sites

The Canadian Arctic covers all Canadian waters north of 60° and also includes Ungava Bay, Hudson Bay, and James Bay (Chan et al. 2012). The Arctic region contains 195 ports, with the Port of Churchill in Manitoba as the major Arctic seaport that is regularly visited by international merchant vessels, which discharge roughly 200,000 m^3 of ballast water annually (Chan et al. 2012). There has been no confirmed report of aquatic NIS in the Canadian Arctic, though research effort in the region is low. The Atlantic coast of Canada and waters of the Estuary and Gulf of St. Lawrence east of Québec City contain over 77 major commercial ports (Casas-Monroy et al. 2014). The region receives more than 23,000,000 m^3 of ballast water released by international merchant vessels each year (Casas-Monroy et al. 2014). At least 112 aquatic NIS have established on the Atlantic Coast of Canada (A. Locke and J. Hanson, unpublished data), though the mechanisms of introduction are not well documented. The Laurentian Great Lakes and the freshwater portion of the St. Lawrence River up to and including Québec

City contain 15 major ports and 121 regional ports (Bailey et al. 2012). The region receives nearly 5,000,000 m^3 of ballast water discharged by international merchant vessels annually (Bailey et al. 2012). The Great Lakes have been invaded by at least 160 aquatic NIS, with ballast water discharge being a dominant vector since 1959 (Bailey et al. 2012). All international merchant vessels carrying foreign ballast water are required to conduct open ocean ballast water exchange (BWE) prior to entering any of the three regions (Government of Canada 2006). The BWE procedure replaces ballast water loaded at port with oceanic water, reducing the density of organisms by purging individuals out of tanks and killing remaining ones by osmotic shock (Bailey et al. 2011).

Sample and data collection

I collected invertebrate samples opportunistically from ballast tanks of trans-Atlantic ships arriving at the Port of Churchill between August and October in 2009 and 2010. Using vertical plankton net tows, I collected samples from one tank per ship. I lowered a 30-cm diameter, 30-μm Nitex plankton net through an opened tank access hatch to the maximum accessible depth inside the ballast tank and retrieved it by hand at a speed of approximately 1 m per second; this process was repeated until at least 1000 L of water was filtered for analysis. Tow depth ranged from 0.5 to 4.6 m with a mean depth of 2.1 m (± 0.2 S.E.M.). I preserved all samples in 95% ethanol and stored them at room temperature until analysis. Temperature and salinity of ballast water were measured within the upper 1 m of the water column of each sampled tank using a thermometer and a digital refractometer, respectively. I sorted and enumerated invertebrates in the laboratory using a dissecting microscope, with individuals identified to the lowest

taxonomic level feasible with the aid of taxonomic experts (see Acknowledgements). Data on invertebrate CP and total PP in ballast water of trans-Atlantic ships arriving at ports in Atlantic Canada and the Laurentian Great Lakes were obtained from DiBacco et al. (2012) and Bailey et al. (2011), respectively. Because 125- and 53-μm plankton nets were used, respectively, to collect ballast water samples in the previous studies, I excluded nauplii and rotifers from my analysis to allow for comparison. In addition, many taxa were not identified to species level, and therefore my results should be considered as conservative estimates of CP. Furthermore, I used data only from ships that took up ballast water at European ports and conducted BWE in the North Atlantic Ocean to reduce the effects of source assemblage on invertebrate CP and total PP (Figure 3.1). The number of invertebrate samples considered in the analysis was 27, 22, and 9 for Arctic, Atlantic, and Great Lakes ships, respectively.

To evaluate the influence of temperature change and ballast water age on CP and total PP of invertebrates, I obtained information from Ballast Water Reporting Forms submitted to Transport Canada on the source, volume, and age of sampled ballast water, as well as date and location of BWE, for each ship. I used the final coordinates of the BWE event as the start point when calculating temperature change and ballast water age (Figure 3.1). This was done because environmental conditions and biological composition may change dramatically during the process of BWE (Gollasch et al. 2000b; Gray et al. 2007; Simard et al. 2011). I calculated temperature change as the difference between ocean surface water temperature at the BWE location and that of sampled ballast water. Because measurement of ballast water temperature during BWE was not available, I interpolated ocean surface water temperature at BWE locations in ArcGIS 10.1 (ESRI

2012) using summer ocean surface water temperature data with a 1° x 1° spatial resolution from the World Ocean Atlas 2009 (Locarnini et al. 2010; Figure 3.1). I defined ballast water age as the number of days between BWE and the sampling event. Two Great Lakes ships were excluded from regressions of CP and total PP on temperature change because of missing BWE dates, locations, or temperature of sampled ballast water. In addition, one Atlantic ship and one Great Lakes ship were excluded from regressions of CP and total PP on ballast water age owing to missing BWE dates.

Statistical analysis

Invertebrate CP and total PP data were log (x + 1) transformed in all analyses to meet assumptions of parametric tests. I used one-way analysis of variance (ANOVA) and post-hoc Bonferroni tests to test for differences in CP and total PP of invertebrates among vessel groups. The relationship between CP and total PP for invertebrates in ballast water for each vessel category was examined using Pearson correlation analysis. To identify factors that might influence CP and total PP of invertebrates in ballast water, I tested for differences in range of temperature change and ballast water age among vessel groups using the nonparametric Kruskal-Wallis test because my data did not follow a normal distribution and homogeneity of variances could not be assumed. I conducted follow-up Mann-Whitney tests with Bonferroni correction when a significant Kruskal-Wallis test result was found. Finally, I conducted multiple regression analyses to investigate the simultaneous effects of temperature change and ballast water age on CP and total PP of invertebrates in ballast water for each vessel group. In two separate analyses using the forced entry method, CP or total PP was entered as the dependent variable, and

temperature change and ballast water age were entered as independent variables. Pair-wise correlation matrix, variance inflation factor (VIF), and tolerance statistics were examined to evaluate multicollinearity in models. A significance level of 95% was used for all statistical analyses. All statistical analyses were conducted using SPSS version 21.0 (IMB Corp. 2012).

3.3 Results

A total of 50 invertebrate taxa were identified from ballast water in trans-Atlantic ships arriving at Port of Churchill, compared to 62 and 25 taxa for those bound for ports on the Atlantic coast and Great Lakes, respectively (Bailey et al. 2011; DiBacco et al. 2012). Copepods represented the majority of all invertebrate taxa in ballast water of Arctic ships (95% of total PP), followed by gastropod larvae (3%). All other major taxonomic groups, such as acarines, amphipods, cladocerans, cirripede larvae, echinoderm larvae, isopods, nematodes, and polychaete larvae, each comprised < 1% of total PP in ballast water of Arctic ships. Similarly, dominant taxa found in ballast water carried by Atlantic ships included copepods (97%), followed by gastropod larvae (1%), with remaining taxonomic groups each consisting of <1% of the total invertebrate abundance. Invertebrate community in ballast water of Great Lakes ships consisted of mainly copepods (92%), while other taxonomic groups each comprised < 1% of total PP.

There were significant differences in CP of invertebrates in ballast water of trans-Atlantic ships arriving at Arctic, Atlantic, and Great Lakes ports (ANOVA, $F_{2, 54} = 19.71$, $p < 0.01$). The Bonferroni post-hoc test revealed that Atlantic ships transported significantly higher invertebrate CP than Arctic and Great Lakes ships ($p < 0.01$ and $p =$

0.03, respectively; Table 3.1 and Figure 3.2). However, I found no significant difference in invertebrate CP between Arctic and Great Lakes ships ($p = 0.16$). Similarly, I noted significant differences in total PP of invertebrates transported by the three vessel categories (ANOVA, $F_{2, 54} = 23.87$, $p < 0.01$). The Bonferroni post-hoc test indicated that Atlantic ships carried significantly greater total PP of invertebrate than Arctic and Great Lakes ships ($p < 0.01$ in both cases; Table 3.1 and Figure 3.2). As with CP, there was no significant difference in total PP between Arctic and Great Lakes ships ($p = 0.50$). I observed a significant positive relationship between CP and total PP of invertebrates in ballast water transported by Arctic and Great Lakes ships, though no relationship was found for Atlantic ships (Figure 3.3).

My data revealed that there was no significant difference in the range of temperature change for vessels traveling different routes to North America (Kruskal-Wallis, $H_2 = 2.75$, $p = 0.25$; Table 3.1). However, I found a significant difference in ballast water age among vessel groups (Kruskal-Wallis, $H_2 = 29.6$, $p < 0.01$). A post-hoc analysis using Mann-Whitney tests with Bonferroni correction showed that Atlantic ships carried significantly younger ballast water than Arctic and Great Lakes ships ($p < 0.01$ in both cases, Table 3.1), while the latter two groups did not differ ($p = 1.0$).

Multiple regression analyses revealed that temperature change and ballast water age explained a total of 26% and 69% of the variation in CP of invertebrates for the Arctic ($F_{2, 24} = 4.27$, $p = 0.03$) and Great Lakes ($F_{2, 4} = 4.41$, $p = 0.10$) regions, respectively, but only 9% for Atlantic ships ($F_{2, 18} = 0.88$, $p = 0.43$). Temperature change was not a significant predictor of CP in any model (Table 3.2). Ballast water age was a better predictor in explaining CP of invertebrates, although it was only significant in the model

for ships destined for Great Lakes (Table 3.2).

A separate multiple regression analysis indicated that temperature change and ballast water age accounted for 47%, 40%, and 26% of variation in total PP of invertebrates transported by Arctic ($F_{2, 24} = 8.55$, $p < 0.01$), Atlantic ($F_{2, 18} = 6.11$, $p = 0.01$), and Great Lakes ($F_{2, 4} = 0.69$, $p = 0.55$) ships, respectively. Total PP was not affected by temperature in any multiple regression models (Table 3.2). Ballast water age was a much more influential predictor for total PP of invertebrates in Arctic and Atlantic ships (Table 3.2). I tested for multicollinearity in all multiple regression models by examining the variance inflation factor (VIF) and found that temperature change and ballast water age were weakly correlated (VIFs = 1.85, 1.10, and 1.19 for the Arctic, Atlantic, and Great Lakes models, respectively).

3.4 Discussion

This is the first study to examine the biological composition of ballast water discharged in Canadian Arctic waters. I compared CP, total PP, and the relationship between these two parameters for invertebrates in ballast water transported by trans-Atlantic ships arriving at ports in the Arctic, Atlantic coast, and the Great Lakes to determine the relative arrival potential of invertebrates via ballast water in the Canadian Arctic. I found that CP and total PP of invertebrates in ballast water transported by Arctic and Great Lakes ships were significantly lower than those for Atlantic ships. Differences in invertebrate CP and total PP among vessel groups appeared to be related to ballast water age, with ballast water carried by Arctic and Great Lakes ships being nearly twice as old as that transported by Atlantic ships. In addition, I detected a significant

relationship between CP and total PP of invertebrates for Arctic and Great Lakes ships, indicating that CP and total PP decreased proportionately as ballast water age increased. In contrast, the absence of such a relationship for Atlantic ships suggests that decreases in total PP were accompanied by little to no reduction in CP. Collectively, assuming higher CP and total PP represent a higher likelihood of introduction, and vice versa, my study suggests that arrival potential of invertebrates in ballast water of Arctic ships may be lower than those of Atlantic ships but similar to Great Lakes ships.

The general negative effect of ballast water age on CP and total PP of invertebrates was expected. Decreasing CP and total PP of ballast water organisms with increasing ballast water age have been reported in a number of previous studies (e.g. Gollasch et al. 2000a; Olenin et al. 2000; Verling et al. 2005; Cordell et al. 2009; Briski et al. 2013, 2014). However, the relationship between total PP and ballast water age was weak for Great Lakes ships. This may be a result of small sample size and limited variation in ballast water age. A post-hoc power analysis conducted in G*Power 3 reveals the statistical power of this analysis was 0.17 (Faul et al. 2007), indicating a relatively poor ability to detect an effect (i.e. high false negative rate). In addition, my study reveals that ballast water age had a greater short-term effect on total PP than on CP of invertebrates. Both CP and total PP decreased as ballast water age increased in Arctic and Great Lakes ships that typically had older ballast water (~15 days). In contrast, a decrease in total PP but not CP was observed in Atlantic ships. In other words, CP and total PP decline at different rates with length of entrainment in ballast water tanks, with CP reducing mainly in older ballast water.

Surprisingly, there were no significant effects of temperature change on CP and

total PP for any of the vessel groups. This may be due to the fact that the trans-Atlantic shipping routes utilized by vessels in this study lie within a relatively narrow latitudinal range (between 30° N and 65° N; Figure 3.1), where ocean temperature variation is minimal, even for Arctic ships, when compared to other oceanic pathways). Taylor et al. (2007) noted that mortality rate of planktonic organisms was significantly higher in ballast water carried by ships that utilize shipping routes spanning temperate to semi-tropical or tropical regions and on trans-equatorial routes than by those travelling within a narrower latitudinal range. Consequently, I view ballast water age, rather than temperature change, as the principal factor influencing CP and total PP of invertebrates, and thus arrival potential of invertebrates via ballast water.

My results suggest that arrival potential of invertebrates via ballast water in the Canadian Arctic may be low, and similar to that in the Great Lakes after implementation of voluntary and mandatory ballast water management regulations in 1989 and 1993, respectively, which required transoceanic vessels with ballast water to conduct BWE a minimum of 200 nautical miles from the coast in water deeper than 2000 m (USCG 1993; Transport Canada 2007). The discovery rate of ballast-mediated NIS in the Great Lakes has declined since the enactment of the ballast water management regulations, with no ballast-mediated invasions reported since 2006 (Bailey et al. 2011). This statistics suggests that managed ballast water released by transoceanic ships poses a low invasion risk for the Great Lakes. BWE is highly effective for the Great Lakes because it replaces coastal organisms entrained at source ports with open-ocean species that are not likely to survive in the freshwater port environment (Gray et al. 2007). The practice may not offer the same degree of protection for the Canadian Arctic because ports there are saline and

thereby lack the harmful osmotic effect that kills mid-ocean organisms when discharging into brackish ports. However, Canada's North may be less vulnerable to ballast-mediated invasions owing to other reasons, in addition to generally low CP and total PP of invertebrates in ballast water due to long voyages. First, the extent of shipping to most Arctic ports is low relative to temperate and tropical locations, thereby constraining the transfer of species (i.e. few introduction events). In comparison, the Great Lakes receive at least 25 times greater volume of ballast water discharged than the Canadian Arctic each year. Second, environmental mismatch, particularly the low temperature, and limited food resources may hinder survivorship, reproduction, and/or population growth of many species in the Arctic (Vermeij and Roopnarine 2008; Ruiz and Hewitt 2009). Temperature differences between BWE locations for Arctic ships and the Port of Churchill ranged from 4.9 to 16.4 °C with a mean temperature of 10.2 °C (± 0.7 S.E.M.). On the contrary, invasion risk of ballast water for the Atlantic region is expected to be much higher than the Arctic and the Great Lakes owing to relatively high CP and total PP of invertebrates in younger ballast water, greater intensity of shipping traffic, as well as better environmental matching owing to the absence of either a salinity or thermal barrier in this area. However, I was not able to determine the invasion rate of ballast-mediated species in the Atlantic region due to a lack of systematic data.

While a majority of past studies assessed arrival potential of invertebrates via ballast water based on total PP (e.g. Lawrence and Cordell 2010; Verling et al. 2010; DiBacco et al. 2012), I acknowledge that biological invasions occur at the population rather than the community level. Therefore, I also evaluated arrival potential of invertebrates via ballast water by comparing mean PP (i.e. dividing total abundance of

invertebrates by the number of invertebrate species in ballast water) across vessel groups. My results would not have been affected had I used mean PP in place of total PP. For example, mean PP was significantly different among vessel groups (ANOVA, $F_{2, 54} = 12.20$, $p < 0.01$), with Atlantic ships transporting a significantly higher mean PP than other ships (Bonferroni post-hoc test, $p < 0.01$). The positive relationship between CP and mean PP was also observed for Arctic (Pearson correlation, $r^2 = 0.23$, $p = 0.01$) and Great Lakes (Pearson correlation, $r^2 = 0.22$, $p = 0.20$) ships, though a significant relationship was observed for the former. The opposite pattern was observed for Atlantic ships (Pearson correlation $r^2 = 0.25$, $p = 0.02$) when mean PP was considered, though this pattern was highly influenced by a single data point, which, if removed, resulted in a non-significant relationship (Pearson correlation, $r^2 = 0.11$, $p = 0.15$).

I recognize by including only vessels that originated from European ports and performed BWE in the North Atlantic Ocean, the approach reduced, but did not eliminate, the potential effect of source assemblage on CP and total PP of invertebrates. Vessels in my study performed BWE over the range from 37° to 61° N in the North Atlantic Ocean, though the geographic midpoints of BWE locations for the different vessel groups were fairly close by: 51°58’44” N and 26°0’10” W, 47°23’10” N and 25°3’18” W, and 48°40’14” N and 21°51’51” W, for Arctic, Atlantic, and Great Lakes ships, respectively (Figure 3.1). Continuous Plankton Recorder (CPR) studies have found pronounced spatial variation in zooplankton richness and abundance in the North Atlantic Ocean, including a decrease in species richness with increasing latitude (Colebrook 1982; Beaugrand et al. 2000, 2001, 2010). In addition, zooplankton communities in the south-western region of the ocean basin increase in diversity during the summer months,

whereas diversity of those in the northern part of the basin remain generally low throughout the year (Figure 5 in Beaugrand et al. 2001). As a result, Arctic ships, which tended to perform BWE at higher latitudes and in colder waters during the summer shipping season, might have collected a less diverse invertebrate assemblage during the BWE process when compared with other vessels. This issue may obscure patterns for Arctic ships.

Although current arrival potential of invertebrates via ballast water may be low in the Canadian Arctic, it will likely increase in the near future due to warming climate and increased shipping activities. Changes in temperature regimes, ocean currents, and other key physical processes associated with climate change are expected to profoundly influence species dispersal and survival (Hellmann et al. 2008; Vermeij and Roopnarine 2008; Wassmann et al. 2011; Floerl et al. 2013). For instance, melting sea ice may increase opportunities for ship-mediated introductions in the Arctic by opening new waterways and shipping channels in the Arctic Ocean as well as extending the length of the shipping season (Niimi 2004; Arctic Council 2009). Once released in post-warming Arctic waters, species may benefit from enhanced survival associated with warmer climate and increased food supply (Vermeij and Roopnarine 2008; Cheung et al. 2009). In addition, future development, including increased extraction of mineral and petroleum resources as well as expanded tourism, will further increase exposure of Arctic ports to ship traffic and the potential for species introduction via ballast water discharge (Arctic Council 2009; Stewart and Howland 2009).

Table 3.1. Summary statistics of colonization pressure, total propagule pressure, range of temperature change, and ballast water age for trans-Atlantic vessels destined for Arctic, Atlantic, and Great Lakes ports. Asterisks denote significant difference ($p < 0.05$) from other vessel categories.

	Arctic	Atlantic	Great Lakes
Colonization pressure (species m^{-3} of ballast water)			
Range	0 – 17	6 – 47	3 – 15
Mean (± S.E.M.)	4.7 (± 0.7)	13.5 (± 1.8)*	6.2 (± 1.2)
Total propagule pressure (individuals m^{-3} of ballast water)			
Range	0 – 9240	213 – 32823	50 – 12122
Mean (± S.E.M.)	942.3 (± 362.7)	13271.6 (± 2381.3)*	2438.6 (± 1282.7)
Temperature change (°C)			
Range	0.04 – 16.4	0.2 – 12.7	5.3 – 9.3
Median	6.5	3.8	6.3
Ballast water age (days)			
Range	8 – 30	3 – 13	8 – 17
Median	15.0	7.0*	14.5

Table 3.2 Summary of multiple regression statistics showing simultaneous effects of temperature change and ballast water age on colonization pressure and total propagule pressure of invertebrates in ballast water transported by ships arriving at Arctic, Atlantic, and Great Lakes ports. Beta denotes the standardized beta coefficient. Asterisks indicate significance at 0.05.

	Arctic		Atlantic		Great Lakes	
	β	p	β	p	β	p
Colonization pressure						
Temperature change (°C)	-0.20	0.42	-0.24	0.33	0.26	0.44
Ballast water age (days)	-0.36	0.14	0.26	0.28	-0.90	0.04*
Total propagule pressure						
Temperature change (°C)	-0.15	0.47	0.16	0.41	-0.33	0.52
Ballast water age (days)	-0.58	0.01*	-0.66	<0.01*	-0.28	0.59

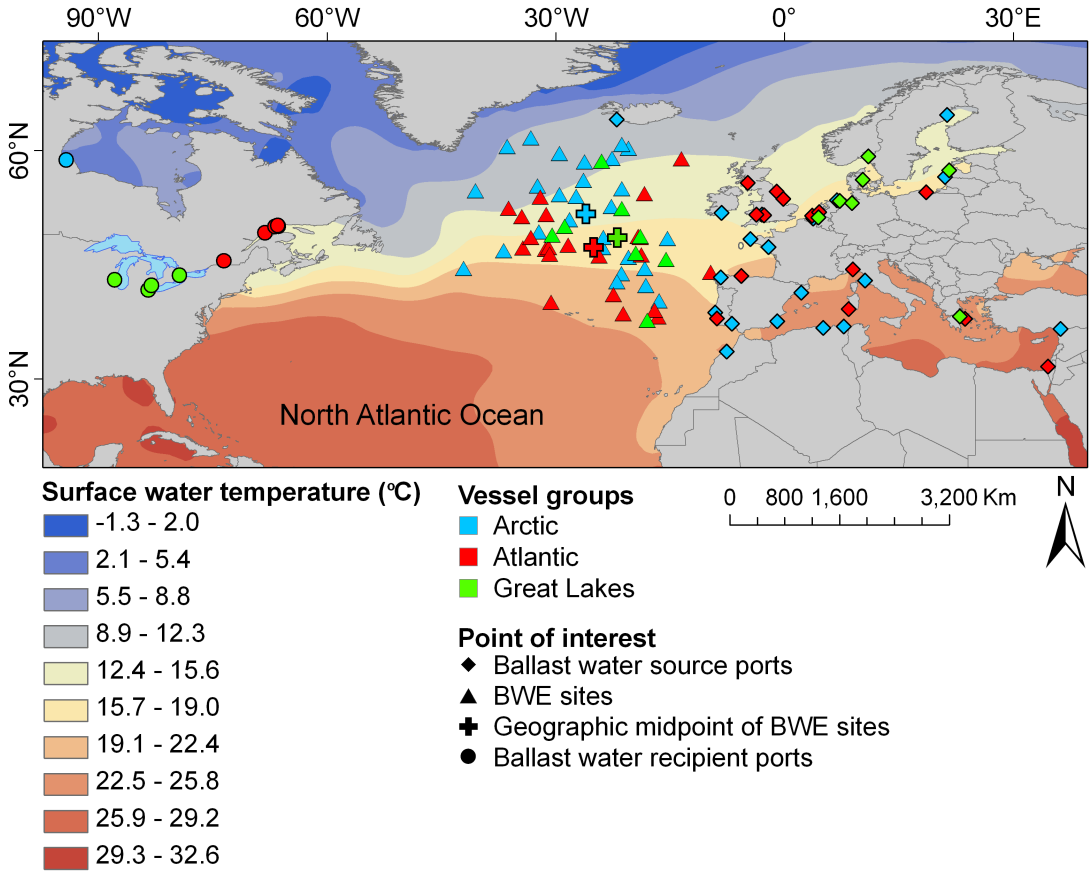

Figure 3.1 Locations of ballast water source (diamond), reported final coordinates of ballast water exchange (BWE) sites (triangle), geographic midpoints of BWE sites (cross), and ballast water recipient ports (circle) for trans-Atlantic ships travelling along Arctic (blue), Atlantic (red), and Great Lakes (green) routes.

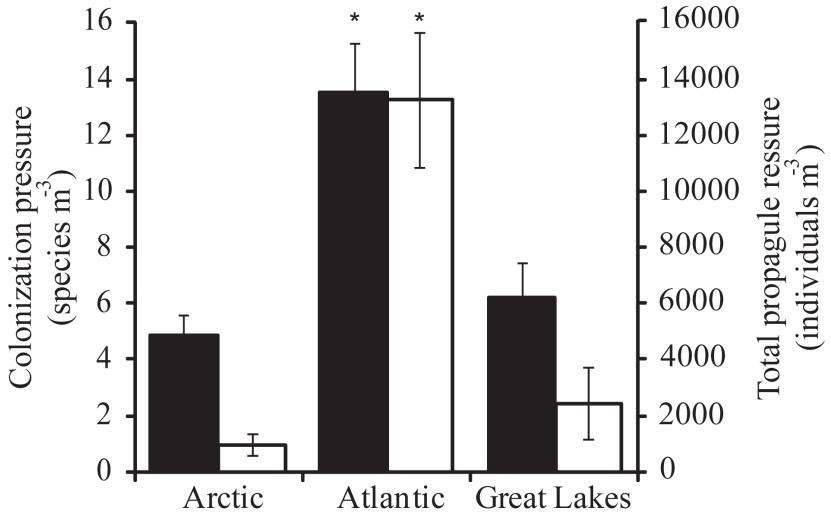

Figure 3.2 Mean colonization pressure (black bar) and total propagule pressure (white bar) of invertebrates in ballast water transported by trans-Atlantic ships destined for Arctic, Atlantic, and Great Lakes ports. Standard errors are included. Asterisk denotes significant difference ($p < 0.05$) from other vessel categories.

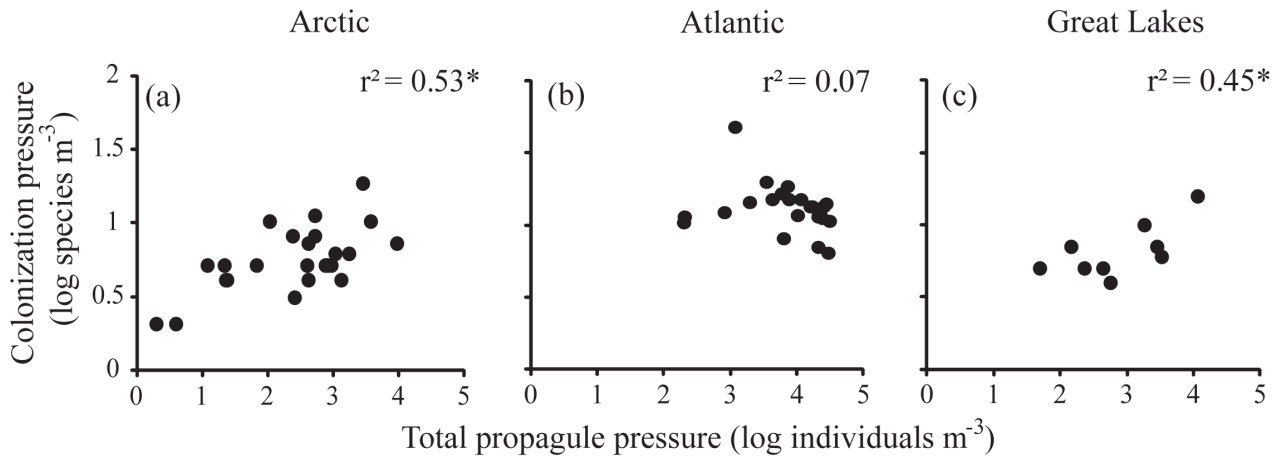

Figure 3.3 Correlation between colonization pressure and total propagule pressure of invertebrates in ballast water collected from trans-Atlantic ships arriving at (a) Arctic, (b) Atlantic, and (c) Great Lakes ports. All data are log-transformed. Asterisks denote significance at 0.05

CHAPTER 4: RELATIVE IMPORTANCE OF VESSEL HULL FOULING AND BALLAST WATER AS TRANSPORT VECTORS OF NON-INDIGENOUS SPECIES TO THE CANADIAN ARCTIC[3]

4.1 Introduction

The global shipping network provides an effective dispersal mechanism that allows nonindigenous species (NIS) to bypass biogeographic barriers and reach areas far beyond their natural distributional range (Seebens et al. 2013). Many marine species foul ships' hulls and can dislodge and/or reproduce at later ports-of-call (e.g. Davidson et al. 2009; Sylvester et al. 2011; Chapman et al. 2013). Similarly, a wide variety of organisms can be loaded when ballast water is taken on board, thus its discharge at subsequent ports can release many individuals of various species into the recipient environment (e.g. Cordell et al. 2009; Simard et al. 2011; Briski et al. 2013). At least 237 marine NIS have been introduced worldwide through hull fouling and the discharge of ballast water, resulting in species extinction, alteration of ecosystem functions, and economic losses in invaded habitats (Molnar et al. 2008). Given the propensity of vessels to transport NIS, including invasive taxa, much research has been conducted on these vectors to reduce transfers via effective vector management (e.g. Coutts et al. 2010; Sylvester et al. 2011; Briski et al. 2013). Very few studies, however, have examined the biological composition of assemblages carried in ballast water of vessels operating in Arctic and sub-Arctic environments (Hines and Ruiz 2000; Chan et al. 2014), and none have addressed fouling

[3] Chan FT, MacIsaac HJ, Bailey SA. Relative importance of vessel hull fouling and ballast water as transport vectors of nonindigenous species to the Canadian Arctic. Submitted to Canadian Journal of Fisheries and Aquatic Sciences (submitted)

biota transported on vessel hulls. In contrast to the Arctic, hull fouling has received far more attention in the Antarctic and sub-Antarctic (e.g. Lewis et al. 2004; Lewis et al. 2006; Lee and Chown 2009).

Although most invasions have been reported in tropical to temperate latitudes where the extent of shipping is greatest, the risk of introducing NIS into northern regions via ship vectors (i.e. hull fouling and ballast water) is expected to increase substantially in the near future owing to climate warming and expanded Arctic shipping (Ruiz and Hewitt 2009; Miller and Ruiz 2014). High-latitude waters have experienced a disproportionate increase in sea surface temperature over the past three decades, resulting in melting sea ice and opening of waterways and shipping channels (Hoegh-Guldberg and Bruno 2010; Smith and Stephenson 2013). For example, the Northern Sea Route between northern Europe and northeast Asia has been traversed regularly by commercial vessels during the summer months since 2009 to save both time and cost of shipping goods (ARCTIS 2014). The Northwest Passage, a similar corridor through the Canadian Arctic Archipelago, was free of pack ice and fully navigable for the first time in recorded history in summer 2007 (Cressey 2007); the first commercial voyage through the passage took place in summer 2013 (McGarrity and Gloystein 2013). In addition, the volume of shipping traffic in the Arctic has increased rapidly as a result of continued expansion of resource exploration, extraction and export, fisheries, and tourism (Miller and Ruiz 2014). Decline in sea ice extent combined with increased development have also led to lengthening of the shipping season (Pizzolato et al. 2014).

New routes, increased intensity, and a prolonged season will enhance the potential to deliver NIS to high-latitude waters by increasing the abundance and diversity of

species (i.e. propagule pressure [PP] and colonization pressure [CP], respectively) transported by vessels. Increasing the number of individuals released per event enhances the likelihood of population establishment owing to reduced demographic constraints, while increasing the number of introduction events enhances establishment probability owing to decreased environmental stochasticity and, possibly, reduced demographic constraints (Taylor and Hastings 2005; Simberloff 2009). Likewise, releasing many species increases the likelihood that at least one will form a reproducing population in the new habitat (Lockwood et al. 2009), where matching environmental conditions between donor and recipient sites provides the greatest potential for establishment (Colautti et al. 2006; Barry et al. 2008; Floerl et al. 2013). Present climatic conditions in certain northern regions are already suitable for temperate species, thus successful establishment may be possible given sufficient propagule supply (de Rivera et al. 2011). Continued climate warming will further improve the level of environmental match between Arctic and global ports, thereby increasing the vulnerability of high-latitude systems to establishment of introduced NIS (Ware et al. 2013).

In this study, I explore the roles of hull fouling and ballast water as transport vectors of NIS to a major Canadian Arctic port located at Churchill, Manitoba. The objectives of the study are as follows: 1) to characterize the composition of assemblages transported on hulls and in ballast water of vessels arriving at Churchill; and 2) to determine the relative importance of hull fouling and ballast water as transfer vectors of NIS to the Canadian Arctic by comparing total abundance of all species (total PP), number of observed species (CP), total abundance of all NIS (nonindigenous total PP), and number of observed NIS (nonindigenous CP) transported per vessel. Because ballast

water biota discharged into Churchill has been partially characterized in a previous study (Chan et al. 2014; Chapter 3), here greater emphasis is placed on investigating those associated with hull fouling. In particular, I examine fouling patterns across various parts of the hull and explore the effects of hull maintenance practices and voyage history on fouling extent on vessels in an Arctic environment. Results of this study can help direct proactive management efforts at the vector that poses the greater risk given limited managerial resources such that relatively pristine Arctic and sub-Arctic ecosystems can be protected from adverse effects of NIS.

4.2 Methods and Materials

Study site

The Port of Churchill (58°46'59"N, 94°13'0"W) is located on the west coast of Hudson Bay, a large inland sea connected to the Arctic Ocean via the Foxe Basin in the north and the Labrador Sea (via Hudson Strait) in the east (Figure 4.1). Mean annual water temperature at Churchill is 4.3 °C (mean range 2.5-8.1°C), with annual salinity averaging 26.3 ppt (Keller et al. 2011). Churchill's primary shipping activity is the export of grain owing to its proximity to the Canadian prairies, and shorter route to ports in Europe and Africa as compared to alternatives (e.g. Port of Thunder Bay; Niimi 2007). Future expansion in shipping is expected as plans exist to increase and diversify commodities imported and exported through the Arctic Bridge Gateway – a seasonal trade route linking Churchill to the Port of Murmansk, Russia (Arctic Bridge Gateway 2014). To date, there have been no ship-mediated NIS reported in the Canadian Arctic, including Churchill, but systematic surveys to detect NIS are very limited (Goldsmit et al.

2014). Within the region, Churchill has been identified as the port at greatest risk of NIS introductions via ship vectors because it receives the largest number of vessel arrivals (about 18 international merchant vessels per year), volume of ballast water discharged (roughly 200,000 m^3 per year), and because its environmental conditions broadly match those of global ports that contain high-impact NIS with which it is connected (Chan et al. 2012, 2013; Chapter 2).

Hull fouling survey

I surveyed hulls of 13 vessels visiting Churchill from August to September of 2010 and 2011. These vessels included nine bulk carriers, two general cargo ships, one roll-on/roll-off vessel, and one supply tug. Sampling was opportunistic, based on availability of ships and tidal currents. I collected and processed hull samples and underwater footage following the procedures outlined in Sylvester and MacIsaac (2010). Briefly, divers surveyed and recorded video of the full length of each vessel's hull, including bulbous bow and stem, sea-chest grating, stern tube, rope guard, propeller nose cone and blades, rudder sides and bottom, as well as leading and trailing edges, and the main hull; divers were not able to inspect the sea-chest grating of six vessels for safety reasons. Sampling was conducted using a stratified sampling design, in which zero (if lacking fouling) to three replicates were haphazardly collected from each underwater location. Divers collected hull samples using a scraper and re-sealable plastic bags or a sampling syringe with a mounted blade. Sampling area of each collection was standardized using a 20 × 20 cm quadrat. Three water samples of *c.* 1 L each at depths corresponding to the waterline, mid-hull, and keel of vessels were also collected to be used as controls; species present in

port water samples were excluded from abundance and richness estimations, potentially resulting in conservative biodiversity assessments. I immediately examined all samples in sorting trays at the surface to determine whether organisms were alive or dead when collected; this analysis was limited to organisms such as amphipods, bivalves, and cirripedes that were large enough to be checked reliably with the naked eye. I sieved hull and port water samples through a 45-μm mesh and preserved them in 95% ethanol at room temperature until analysis. Information including ship particulars and plans, date of last dry-docking and anti-fouling paint application, and the last 10 ports-of-call was obtained from vessels' personnel.

I processed and enumerated hull samples in the laboratory using a dissecting microscope, with individuals identified to major taxonomic groups. A minimum of 30 individuals per morphotypes were collected and identified to the lowest taxonomic level feasible with the aid of taxonomic experts (Sylvester and MacIsaac 2010; see Acknowledgement). Many individuals were not identified to the species level; thus my analysis may underestimate the true species richness of transported assemblages (the same applies to ballast water samples; see below). In all samples, algal cover was limited to relatively thin films lacking reproductive structures; therefore, I focused my efforts on invertebrates and considered algae mainly as potential habitat for invertebrates. I classified identified taxa into five categories based on their known occurrences: 1) Hudson Bay: taxa that have previously been reported in Hudson Bay; 2) Canadian Arctic: those that are absent from Hudson Bay but have been recorded elsewhere in the Canadian Arctic, including all waters north of 60° and those in Hudson Bay, James Bay, and Ungava Bay (Canadian Coast Guard 2014); 3) Arctic: those that have not been found in

the Canadian Arctic but are known elsewhere in the Arctic, which is defined as "areas within the seasonally-averaged 2°C surface isotherm or the median maximum sea-ice extent, whichever is greater" (Figure 4.1; Sirenko et al. 2014); 4) non-Arctic: those that have known distributions outside of the Arctic; and 5) unknown: those whose distribution could not be determined because they were not identified to species level. For the purpose of the study, Hudson Bay species were considered as native to Churchill, while Arctic and non-Arctic species were treated as NIS. Canadian Arctic species were classified as cryptogenic because their invasion status could not be determined with confidence due to insufficient baseline biodiversity information for Canada's Arctic coastal systems (see Archambault et al. 2010; Goldsmit et al. 2014). Determination of taxa distributions was based on an extensive literature review of scientific journal publications, taxonomic keys, government reports, and online biodiversity databases, as well as consultation with taxonomic experts (Supplementary Table S4.3). In addition, I determined the potential survival for NIS if released into Churchill based on thermal and salinity tolerances documented in the literature (Supplementary Table S4.3).

To estimate total PP (or nonindigenous total PP) per vessel, I used abundance data from hull samples combined with percent cover information obtained from video footage (Sylvester and MacIsaac 2010). I obtained 30 still images from one to one-and-a-half hours of footage per vessel using a stratified random design, ensuring that all underwater locations were examined. I superimposed a 100-point grid over images to estimate percent cover. I also calculated the surface area of each underwater location by approximating each location to simple geometric forms using technical information from ship particulars and plans (Sylvester and MacIsaac 2010). I estimated abundances per

location by multiplying average abundances in hull samples by the location's percent cover and surface area, then dividing by the surface area of the sampling quadrat (0.04 m^2). Total PP per vessel was then obtained as the sum of abundances in all locations.

Ballast water sampling

I opportunistically sampled ballast water of 32 vessels, including 28 bulk carriers and four general cargo ships, arriving at Churchill between August and October of 2009 and 2010. Four of these vessels, all bulk carriers, were also surveyed for hull fouling in 2010. I collected invertebrate samples from one tank per ship before ballast water was discharged. Five baseline harbour water samples, roughly 1000 L each, were also collected using plankton net tows (30-cm diameter, 30-μm mesh). Methods for sample collection, enumeration, and taxonomic identification are detailed in Chan et al. (2014) and Chapter 3. Preserved organisms were assumed alive at the time of collection if they appeared to be in good condition when examined in the laboratory. Identified taxa were grouped into five categories using the same criteria described previously. Taxa present in harbour water samples were considered native to Hudson Bay.

To estimate total PP (or nonindigenous total PP) in ballast water per vessel, I multiplied abundances observed in samples by the volumes subsequently discharged into Churchill. In four cases, the proposed discharge volume included ballast water from two different sources. I assumed that collected samples were representative of ballast water from both sources because ballast was loaded on board at neighbouring ports within a short period of time (< five days) and was exchanged in the North Atlantic Ocean.

Statistical analyses

To evaluate whether sampling effort was adequate in characterizing the true species richness in hull fouling and ballast water assemblages, I estimated asymptotic species richness for each ship sampled using Chao-2 and Chao-1 species richness estimators, respectively. Chao-2 richness estimator is recommended for replicated incidence or abundance data collected over a heterogeneous habitat, such as the hull fouling survey in this study, whereas Chao-1 is suitable for abundance data collected from a single representative sample from a community, as was the case with ballast water sampling (Gotelli and Colwell 2011). Chao-1 and Chao-2 species richness estimations were conducted using EstimateS version 9.1.0 (Colwell 2013).

I used independent t-tests to explore differences in total PP and CP for invertebrates transported on vessels' hulls versus those in ballast water, assuming that the two vectors operated independently (see Hewitt et al. 2009). Data were log (x + 1) transformed to meet assumptions of parametric tests. Separate t-tests were performed for four vessels from which both hull and ballast water samples were collected for a direct comparison of the vectors for the same vessels. Similar analyses were conducted to compare the same variables between vectors using data from all sampled vessels (n = 45). Post-hoc power analyses were conducted in G*Power 3 to estimate statistical power achieved with various sample sizes (Faul et al. 2007). I compared nonindigenous total PP and nonindigenous CP between two vectors using Mann-Whitney U tests because the data did not follow a normal distribution. Again, separate Mann-Whitney U tests were performed for comparisions within ships (n = 4), and comparisions across ships (n = 45). In addition, I examined the relationship between CP and total PP, and between

nonindigenous CP and nonindigenous total PP for hull fouling and ballast water assemblages using Pearson and Spearman's correlation analyses, respectively. Vessels carrying no individuals were excluded from analyses because no relationship is expected when inoculum size is small (see Lockwood et al. 2009; Briski et al. 2012). Analyses using observed (i.e. CP and nonindigenous CP) and estimated (i.e. Chao-1 and Chao-2) richness were conducted and provided qualitatively similar results, thus only results obtained using the former are presented consistent with previous studies (e.g. Briski et al. 2012; Chan et al. 2014).

To examine fouling patterns on vessels, I tested for differences in percent cover across underwater locations on the hull using the non-parametric Kruskal-Wallis test. Parametric tests were not used because data did not follow a normal distribution and homogeneity of variances could not be assumed. I also compared species richness among locations using Chao-2 richness estimate, where non-overlapping 95% confidence intervals denote significant statistical differences. Sampled-based rarefaction curves were generated to standardize richness across locations on the basis of a common number of samples (Gotelli and Colwell 2011).

I conducted a series of simple linear regression analyses to test the effects of hull maintenance practices and voyage history on fouling extent on vessels. Total PP, CP, and Chao-2 richness estimate were included as response variables, whereas age of anti-fouling paint, total port residence time (in the last 10 ports-of-call), and number of bioregions visited (during the last 10 voyages) were treated as predictor variables. Ports were grouped into nine bioregions following the Marine Ecoregions of the World (Spalding et al. 2007), which included the Arctic, Central Indo-Pacific, Temperate North

Atlantic, Temperate North Pacific, Temperate South Africa, Temperate South America, Tropical Atlantic, and Western Indo-Pacific, as well as the Laurentian Great Lakes (Figure 4.1). While sailing speed can be a key determinant of fouling extent (Coutts et al. 2010; Sylvester et al. 2011), it was excluded from analysis because of the relatively low values (~10 knots) and minimal variability among vessels. All statistical analyses were conducted using SPSS version 22.0 (IMB Corp. 2013) unless otherwise stated.

4.3 Results

Vessels surveyed for hull fouling visited both foreign and domestic ports prior to their arrivals at the Port of Churchill (Figure 4.1). Typical sailing speed of vessels ranged from 7.0 to 11.2 knots (mean 9.9 knots). Wetted surface area ranged between 496 and 6,782 m^2 (mean 5,428 m^2). Time since last dry-dock and anti-fouling paint application varied from 129 to 698 days (mean 392 days). Percent fouled surface area was variable, ranging from 0.0 to 28.1% (mean 4.3%). Total PP in hull fouling assemblages varied from 0.0 to 3.3 $\times 10^6$ individuals per vessel, with a mean of 4.9×10^5 individuals. Chao-2 richness estimate averaged 29.4 species per vessel, with a maximum of 79.4, and was 2.7 times higher than the mean observed CP (11.0 species).

I identified 86 distinct invertebrate taxa from hull samples, excluding taxa found in port water (Supplementary Table S4.1). Cirripedes represented the majority of all fouling taxa (92% of total PP per vessel), followed by nematodes (4%) and copepods (2%) (Figure 4.2). Cirripedes and copepods were also the most species-rich taxonomic groups, followed by nematodes (Figure 4.2). There were 15 non-Arctic taxa, including 11 cirripede, one cladoceran, two copepod, and one nematode taxa (Supplementary Table

S4.1). Seven of these species were well-recognized hull fouling NIS that have established elsewhere in the world, including *Amphibalanus amphitrite*, *Amphibalanus eburneus*, *Amphibalanus improvisus*, *Amphibalanus reticulatus*, *Austrominius modestus*, *Balanus trigonus,* and *Megabalanus coccopoma*. Live specimens were found for the first six species, which accounted for 0.3%, 25%, 93%, 17%, 100%, and 100%, respectively, of total abundance of each of these species. However, only *A. amphitrite*, *A. eburneus*, *A. improvises*, and *A. modestus* have the potential to survive if propagules are released into Churchill based on their known temperature and salinity requirements. Tolerance information was not available for two copepods, *Paronychocamptus huntsman* and *Schizopera clandestine*, and one nematode, *Prochromadora orleji*; these species are commonly found in cold temperate, coastal waters and thus may have the ability to tolerate environmental conditions in Churchill. With the exception of *M. coccopoma, Megabalanus* cf. *spinosus*, and *Megabalanus* cf. *tintinnabulum*, for which only empty shells were found, as well as the freshwater cladoceran *Acantholeberis curvirostris*, all remaining non-Arctic taxa may survive if released into the port environment. Furthermore, I found two Arctic amphipod species, *Crassicorophium bonellii* and *Jassa marmorata*, and one nematode taxon, *Geomonhystera* sp., which have not yet been reported in the Canadian Arctic and could potentially survive in Churchill.

Between 5,696 and 26,718 m^3 of ballast water per vessel (mean 10,456 m^3) was discharged at Churchill during the sampling period. The majority of this water originated from foreign ports in the Temperate Northern Atlantic and was exchanged in the North Atlantic Ocean, except for one case, in which it was taken from another Canadian Arctic port (Deception Bay) and was not exchanged (Figure 4.1). Total PP in ballast water

varied from 0.0 to 1.6 $\times 10^8$ individuals per vessel, with a mean of 1.7 $\times$ 10^7 individuals. Chao-1 richness estimate averaged 5.3 species per vessel, with a maximum of 20.0, and was very similar to observed CP (mean 5.1 species).

Invertebrates in ballast water samples belonged to 58 distinct taxa (Supplementary Table S4.2). Copepods (80%), rotifers (16%), and gastropods (2%) made up the largest contributions to total PP per vessel (Figure 4.2). Copepods also represented the most diverse taxonomic group, followed by nematodes and gastropods (Figure 4.2). I found two non-Arctic species, a copepod, *Nitokra lacustris,* and a nematode, *Daptonema tenuispiculum*; however, they are not likely to survive if released into Churchill. I observed five Arctic taxa (two copepod species, *Centropages typicus* and *Heterolaophonte ströemi*, and three nematode taxa, *Ascolaimus* sp., Axonolaimidae, and *Geomonhystera* sp.) that could tolerate environmental conditions in Churchill.

When considering only the four vessels from which both hull and ballast water samples were collected, total PP was significantly lower for hull fouling than for ballast water assemblages ($t_6 = -2.94$, $p = 0.03$), while CP did not differ between the two vectors ($t_6 = 0.32$, $p = 0.76$). Statistical power for the two t-tests was 0.69 and 0.06, respectively. There were no differences in nonindigenous total PP and nonindigenous CP between vectors within the same vessels ($U_8 = 2.0$, $p = 0.11$ in both cases). When all vessels were considered, total PP was significantly lower for hull fouling than for ballast water ($t_{43} = -4.37$, $p < 0.05$), whereas CP did not differ between vectors ($t_{43} = 0.96$, $p = 0.34$). Statistical power for the two t-tests was 0.97 and 0.13, respectively. In contrast, both nonindigenous total PP and nonindigenous CP were significantly higher on hulls than in ballast water of vessels ($U_{45} = 139.0$, $p = 0.04$ and $U_{45} = 117.0$, $p < 0.01$, respectively),

suggesting a greater potential introduction risk for the former vector. There was a significant positive relationship between CP and total PP as well as nonindigenous CP and nonindigenous total PP for hull fouling assemblages (Figure 4.3). Similarly, CP was positively correlated with total PP for ballast water assemblages; however, such a relationship was not observed when considering only NIS (Figure 4.3).

Percent fouled area varied significantly across different underwater vessel locations ($H_8 = 15.19$, $p < 0.05$). Propellers and sea-chest gratings were typically most heavily fouled relative to other locations (Figure 4.4a). However, Chao-2 richness estimate did not vary significantly by location (Figure 4.4b); sample-based rarefaction curves confirmed that this finding was not due to differences in sample size across locations (not shown). None of the variables considered – including age of anti-fouling paint, total port residence time, or number of bioregions visited – were significant predictors of total PP, CP, or Chao-2 richness estimate ($p > 0.05$ in all cases).

4.4 Discussion

This study provides the first quantitative, comparative assessment of two potent transport vectors of NIS (i.e. hull fouling and ballast water) on the same vessels and is the first to examine fouling assemblages transported on hulls of vessels operating in an Arctic environment. Results from this study indicate that both hull fouling and ballast water are active vectors for delivering marine species to the Canadian Arctic. Hull fouling, however, appears to be the more important vector for delivery of NIS. While I did not find significant differences in total PP and CP for NIS between vectors within the same vessels, likely owing to the small sample size ($n = 4$), both nonindigenous total PP

and nonindigenous CP were significantly higher for hull fouling than for ballast water when comparing vectors across vessels (n = 45). Additionally, more heavily fouled vessels tended to transport a greater number of NIS, as indicated by the significant positive relationship between nonindigenous CP and nonindigenous total PP. Such a relationship was not detected for ballast water, suggesting that nonindigenous CP could be low despite high nonindigenous total PP. Therefore, the likelihood of transferring multiple species during a single transport event appears higher for hull fouling than for ballast water.

The discovery of live specimens belonging to six widespread nonindigenous barnacles – *Amphibalanus amphitrite*, *Amphibalanus eburneus*, *Amphibalanus improvises*, *Amphibalanus reticulatus*, *Austrominius modestus*, and *Balanus trigonus* – on vessels arriving at Churchill further underscores the importance of hull fouling as a vector for delivering NIS to the Canadian Arctic. It was not possible to determine the origin of these species because they have widespread distributions (Carlton et al. 2011), and individuals could have accumulated on a ship's hull from different sources over time. These species were found on vessels that had travelled to Temperate North Atlantic, Temperate South Africa, Temperate South America, Tropical Atlantic, and West Indo-Pacific bioregions, demonstrating their ability to survive on hull surfaces during transoceanic voyages to high-latitude waters despite extensive longitudinal, latitudinal, and environmental changes. This finding appears to provide the first record of temperate fouling NIS surviving transit to a sub-Arctic port. *A. amphitrite*, *A. eburneus*, *A. improvises*, and *A. modestus* could potentially survive if introduced into Churchill, though whether they could establish self-sustaining populations is unknown (Fofonoff et

al. 2003b; O'Riordan 2009). Temperate fouling NIS have also been found alive after long voyages to sub-Antarctic environments, highlighting the potential of transferring NIS on vessel hulls from temperate to sub-polar regions (Lewis et al. 2006; Lee and Chown 2009). In comparison, no temperate NIS capable of surviving environmental conditions in Churchill were found in ballast water, though there were a few Arctic NIS that have not yet been reported in the Canadian Arctic.

Operational features of hull fouling and ballast water could contribute to the relative importance of the vectors in transferring marine species. Fouling taxa can attach to hull surfaces at any time, most typically when vessels are in port, whereas ballast-mediated organisms are taken on board only when vessels load ballast (Hewitt et al. 2009). Greater nonindigenous total PP and nonindigenous CP observed for hull fouling than ballast water assemblages could result from the fact that vessels visited a number of global ports prior to Churchill, thereby exposing their hulls to a menagerie of species from a wide variety of source communities. In contrast, vessels took up ballast water only at one or two source ports, thereby limiting the sources and diversity of organisms loaded with ballast water. Additionally, relatively complex assemblages comprised of benthic, sessile and mobile taxa were found on vessel hulls. Sessile taxa, such as bivalves and cirripedes, can provide structural habitat and protection for mobile organisms against sheer forces, thereby enhancing species diversity (Davidson et al. 2009). Conversely, mainly holoplankton and planktonic larvae of benthic species were observed in ballast water. However, after arriving at Churchill, hull-borne organisms must be dislodged or reproduce in order to be introduced, thus the actual total PP and CP, including nonindigenous total PP and nonindigenous CP, released into the port environment are

extremely difficult to quantify. In contrast, ballast water is far more straightforward, as almost all individuals carried in ballast water will be discharged into the harbour (Fofonoff et al. 2003a). Considering the volume of water released into Churchill, ballast water discharge may introduce substantial total PP and CP into the receiving environment. However, the potential for introducing ballast-mediated NIS appears rather low owing to low nonindigenous total PP and nonindigenous CP found in ballast water of sampled ships.

Current management regimes for hull fouling and ballast water could also influence the relative role of the vectors by altering survivorship of organisms during transport. It is often assumed that organisms transported on ships' hulls have lower survivorship than those in ballast water because fouling taxa are directly exposed to the ambient environment and can experience extreme wave turbulence and fluctuations in water temperature and salinity during transoceanic voyages (Fofonoff et al. 2003a; Davidson et al. 2008). Conversely, organisms in ballast tanks are relatively protected from the external environment (Fofonoff et al. 2003a), though they may suffer high mortality within tanks owing to starvation, predation, light and oxygen limitation, or toxicity associated with antifouling applications (Carlton 1985; Gollasch et al. 2000b; Wonham et al. 2001). Nevertheless, a rather high fouling cover (10-28%) was found on certain vessels, suggesting that existing anti-fouling practices are not sufficient to manage hull fouling. Although the International Maritime Organization (IMO) has introduced Guidelines for the Control and Management of Ships' Biofouling to Minimise the Transfer of Invasive Species (IMO 2011), hull maintenance remains a voluntary practice in Canada, carried out by vessel owners with the aim of reducing hydrodynamic drag and

fuel consumption. On the other hand, all ballast water originating from foreign sources was exchanged in mid-ocean, as required by Canada's mandatory ballast water management regulations (Government of Canada 2006). Ballast water exchange replaces coastal water loaded at ports with oceanic water, purging most coastal organisms and killing remaining ones via osmotic shock (Bailey et al. 2011). The procedure is documented as 70-95% effective in removing original coastal organisms (Ruiz and Reid 2007; Cordell et al. 2009). This may further contribute to the relatively low nonindigenous total PP and nonindigenous CP observed in ballast water, while total PP remained high, possibly due to the presence of oceanic species picked up during exchange.

The relative contribution of hull fouling versus ballast water to NIS introductions varies across systems. Results from this and previous studies suggest that hull fouling is a more prevalent transport vector than ballast water in sub-polar environments (i.e. sub-Arctic and sub-Antarctic) (Lewis et al. 2003; Lee and Chown 2009). Globally, hull fouling has also been implicated in a greater number of established NIS than ballast water in coastal regions of Australia and New Zealand (Hewitt et al. 2009), Brazil (Farrapeira et al. 2011), and the North Sea (Gollasch 2002b). In Canada, however, ballast water is a stronger vector than hull fouling in terms of total PP and CP transported to the Atlantic and Pacific coasts (Sylvester et al. 2011). Ballast water, rather than hull fouling, is also considered to be the dominant transfer vector of NIS to the Great Lakes due to the salinity barrier imposed on fouling organisms (Sylvester and MacIsaac 2010).

Future changes in shipping activities are expected to alter the relative importance of hull fouling and ballast water in the Canadian Arctic. Over 25 large-scale mineral,

offshore oil and gas, offshore energy, and infrastructure development projects have been planned for the region, some of which may be operational by 2020 (Gavrilchuk and Lesage 2014). These projects would lead to about 433 additional shipments per year, significantly increasing shipping traffic in Canada's North from the current level of 599 arrivals per year (Chan et al. 2012; Gavrilchuk and Lesage 2014). A single proposed project is expected to result in discharge of between 70,000 to 200,000 m^3 of ballast per shipment into Canadian Arctic waters (Stewart et al. 2012). While the potential for both hull- and ballast-mediated transfers of NIS will clearly increase as a result of these proposed developments, the risk for the latter may increase to a greater extent than the former. Larger volume of ballast water carried by such vessels will likely lead to a proportional increase in total PP and CP of ballast-mediated organisms transferred, whereas greater wetted surface area does not necessarily result in a direct increase in total PP and CP of fouling organisms transported on hulls because surface area of fouling 'hot spots' like the propeller and sea-chest will remain low.

Identifying factors that may influence total PP and CP associated with hull fouling and ballast water can improve our ability to manage these vectors. Within individual vessels, I found that fouling (i.e. total PP) was not uniformly distributed across the hull, with sea chest gratings and propellers tending to have higher fouling cover than other underwater vessel locations. CP, however, did not vary significantly across locations. This finding is generally consistent with a number of studies in which niche areas – topographically complex locations such as propeller, rudder, and sea chest grating – were reported to be more heavily fouled than the main hull (e.g. Coutts and Taylor 2004; Davidson et al. 2009; Sylvester and MacIsaac 2010). Fouling extent also varied across

vessels, yet it is not clear what contributed to these patterns. None of the variables examined, including age of anti-fouling paint, total port residence time, and number of bioregions visited, were related to total PP and CP for hull fouling assemblages. Previous studies have found that vessels with older anti-fouling paint supported richer fouling assemblages than those that were recently painted because effectiveness of anti-fouling paint decreases with time (Davidson et al. 2009; Sylvester et al. 2011). Additionally, vessels that spend more time in ports accumulate greater fouling because longer residency provides greater opportunity for organisms to colonize hull surfaces (Davidson et al. 2009; Sylvester and MacIsaac 2010; Sylvester et al. 2011). A positive relationship between diversity of fouling assemblages and the number of bioregions visited by vessels have also been observed, possibly as a result of greater exposure to a wide variety of biological communities (Sylvester et al. 2011). The absence of a significant relationship between fouling variables and vessel characteristics in this study may be due to the small sample size. Alternatively, the effects of these variables on fouling extent could be obscured by Churchill's sub-Arctic environment, particularly the presence of sea ice. Ice scouring removes or negatively impacts fouling assemblages on vessels and plays a crucial role in determining fouling extent in high-latitude waters (Lewis et al. 2004; Lee and Chown 2007; Sylvester et al. 2011). Data from Canada Ice Services (2014) indicate that sea ice was present in the Hudson Strait and Labrador Sea during this study period, thus ice scouring is possible. By contrast, total PP and CP transported in ballast water were negatively related to age of ballast water (see Chan et al. 2014; Chapter 3).

Because of the nature of the transport vectors, substantially different sampling methods were used to collect samples from hulls and ballast water. I followed standard

methods, ensuring each vector was surveyed appropriately. Differences in methodologies may, however, lead to biases in results. For example, ~10 replicates were collected across different parts of the hull to cover the range of habitats that may support fouling species. In contrast, only one ballast water sample was collected from one tank per ship because repeated vertical plankton hauls are adequate in collecting invertebrates from the entire water column inside a ballast tank (Gray et al. 2007) and the collected sample is expected to be representative of all ballast water on board (see methods). Indeed, matching observed and estimated (Chao-1) species richness values for ballast water assemblages suggests that sampling effort is adequate for characterizing the full extent of biodiversity in ballast water, whereas discrepancy between observed and estimated (Chao-2) richness indicates the opposite for hull fouling. Additionally, sample size for hull fouling (n = 13 ships) was smaller than that for ballast water (n = 32 ships) due to constraints imposed by ships' operations, weather conditions, schedules of SCUBA divers, and cost. Thus, ballast water sampling may have been more likely to detect the array of inter-vessel biodiversity differences than sampling conducted on vessel hulls.

The Arctic is one of the most pristine ecosystems on earth (CAFF 2013). Arctic coastal environments are, however, under unprecedented threats from NIS due to a combination of climate change, resource development, and the growth of Arctic shipping (Miller and Ruiz 2014). This study reveals that diverse marine communities are transported on hulls and in ballast water of vessels travelling to the Canadian Arctic. In particular, a number of viable, widespread nonindigenous barnacle species were found in fouling assemblages, highlighting the prominence of hull fouling over ballast water as a transport vector of NIS. Hull fouling in Arctic environments may differ substantially

from that in temperate locales in two key ways. First, even with moderating environmental conditions, it is unclear whether species transported to the Arctic during summer can survive ambient conditions, notably during winter months. Secondly, polar waters may contain fragmented ice sheets, which could abrade species fouled on exposed sections of vessels, potentially introducing individuals into waters that they would otherwise be unlikely to be introduced into. In closing, it is important to recognize that the relative importance of hull fouling and ballast water as transport vectors of NIS may vary in response to changes in shipping patterns, vector management regimes, and environmental conditions, thus attention should be given to both transport vectors.

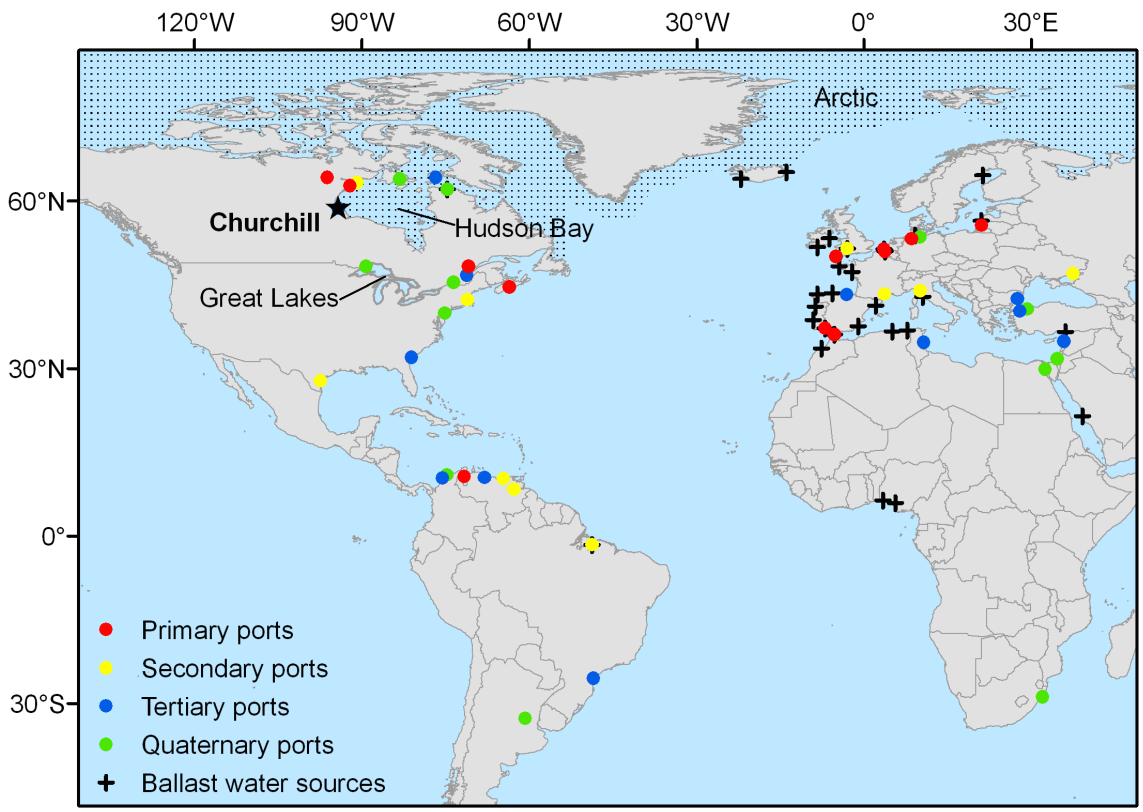

Figure 4.1 Map illustrating ports-of-call visited by vessels during the last four voyages preceding hull fouling surveys in Churchill. Primary ports (red circles) are origins of non-stop voyages to Churchill. Secondary (yellow circles), tertiary (blue circles), and quaternary (green circles) ports are those visited by vessels immediately before primary, secondary, and tertiary ports, respectively. Note data from past 10 voyages were used in analyses, but only last four ports-of-call visited are presented for brevity. Sources of sampled ballast water (black crosses) are also shown. The Port of Churchill is indicated by a black star. Dot hatch pattern defines the Arctic region, following Arctic Register of Marine Species (Sirenko et al. 2014).

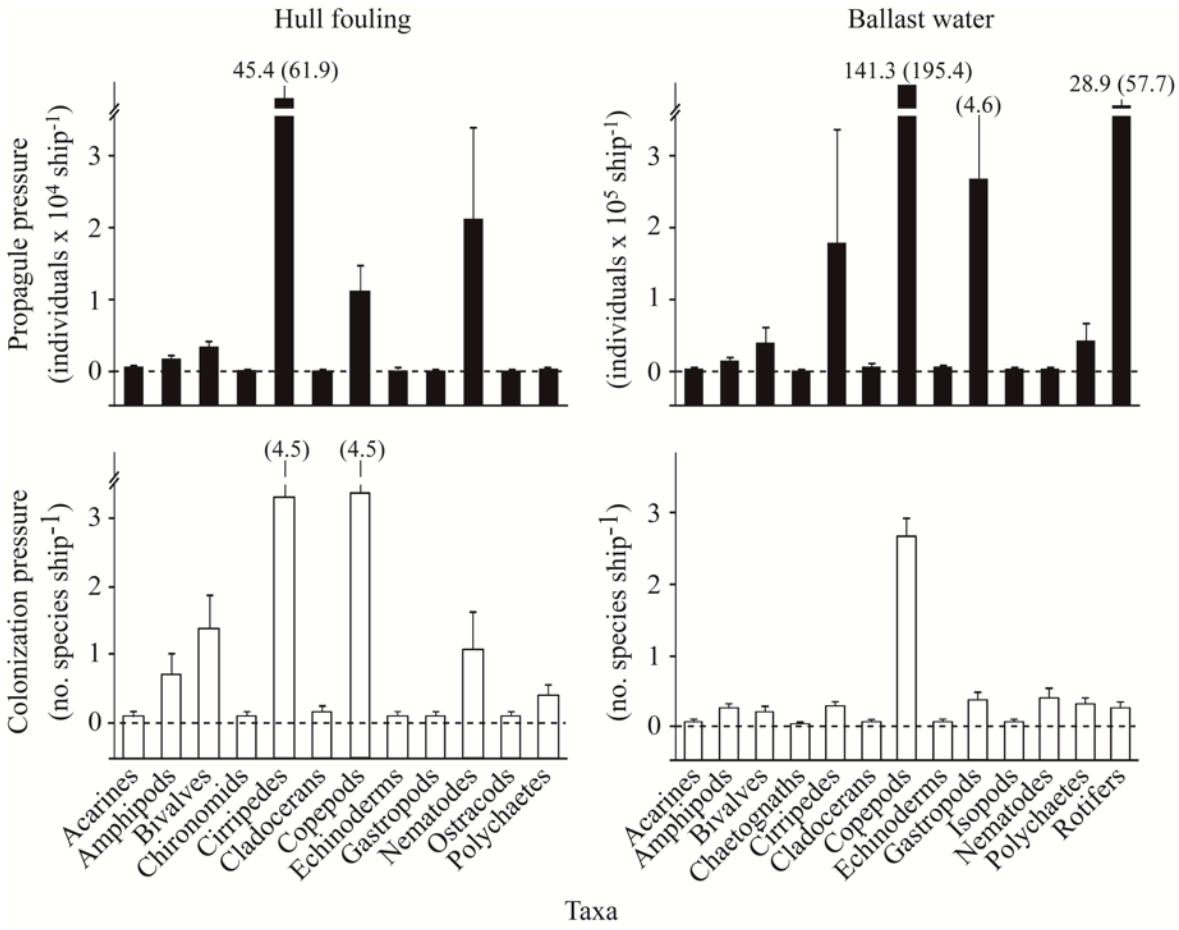

Figure 4.2 Mean propagule pressure (black bars) and colonization pressure (white bars) of invertebrate taxa estimated in hull fouling (left panels) and ballast water (right panels) assemblages transported per vessel. Values off the scale are indicated. Standard errors are also included, in parentheses when off scale. Note the differences in scale and taxa group among plots.

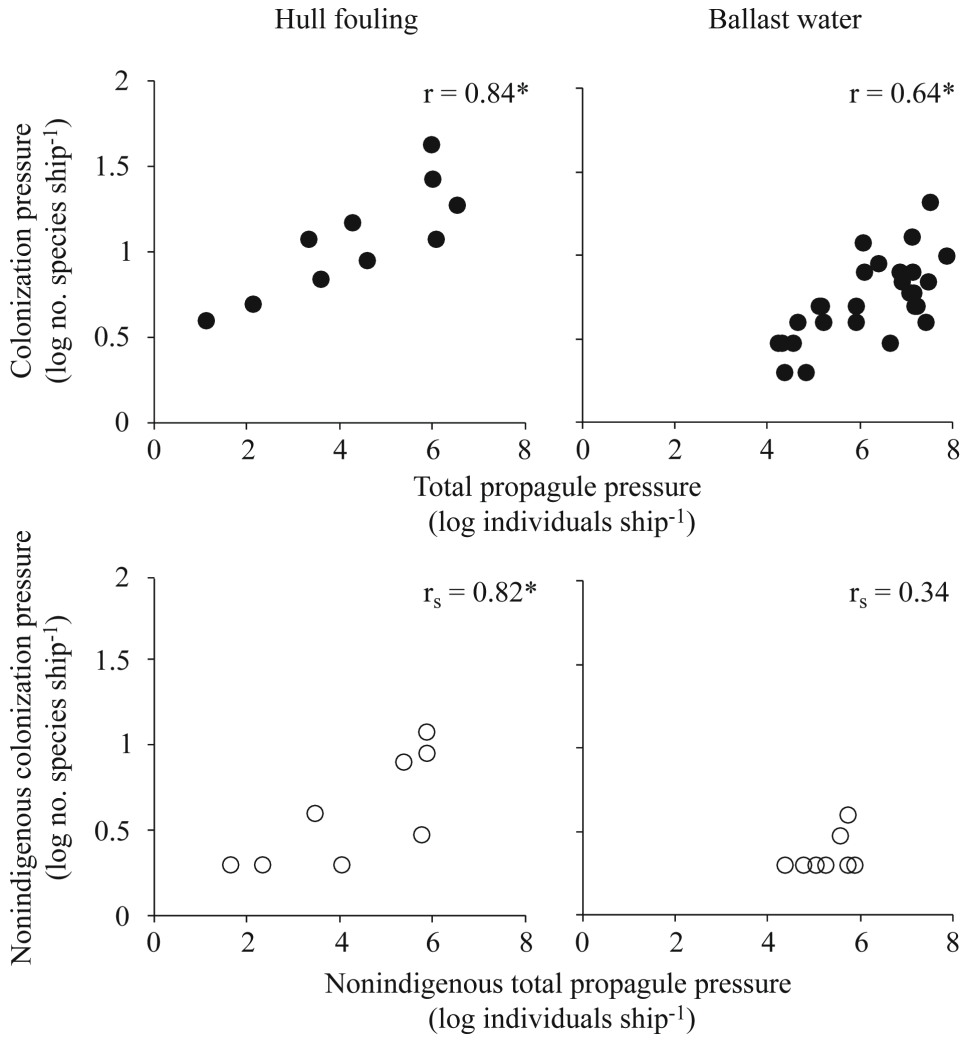

Figure 4.3 Correlations between colonization pressure and total propagule pressure (black circles), and between nonindigenous species (NIS) colonization pressure and total NIS propagule pressure (white circles) for hull fouling (left panels) and ballast water (right panels) assemblages transported per vessel. All data are log-transformed. Asterisks denote significance at 0.05.

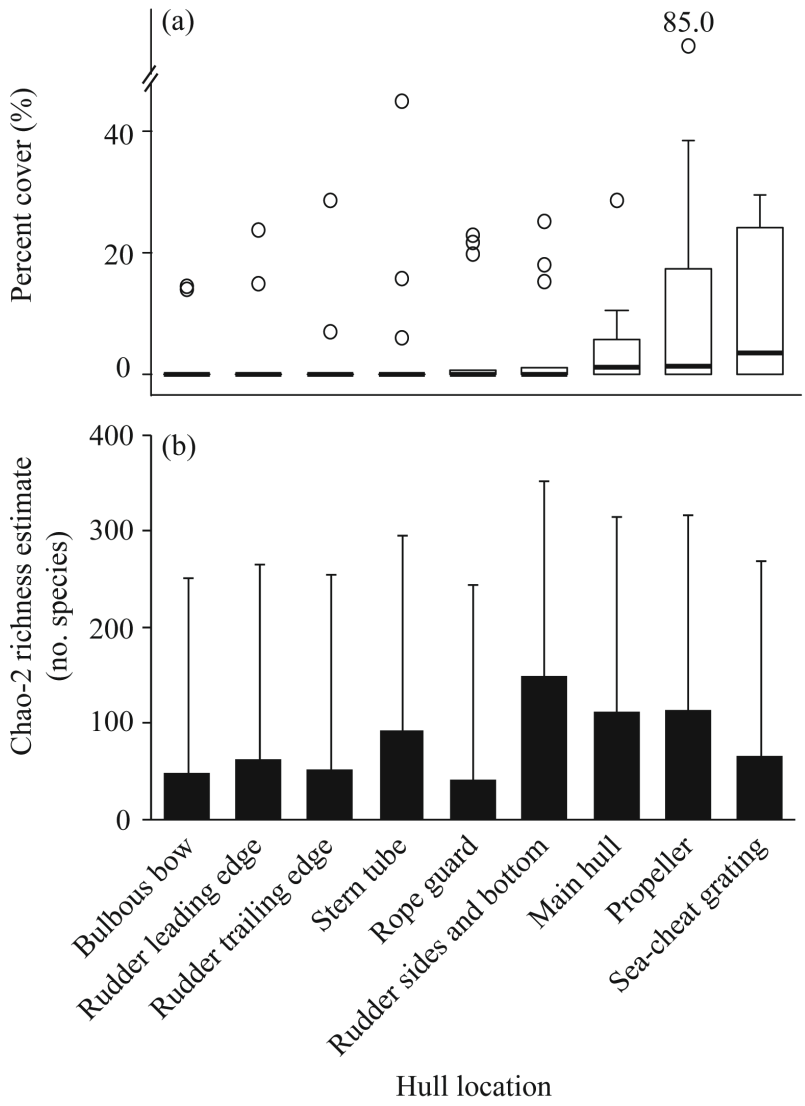

Figure 4.4 Median percent cover of fouling (a) presented as Tukey box-whisker plots and Chao-2 species richness estimate (± 95% C.I.) (b) for underwater locations across all vessels. Value off the scale is indicated.

4.5 Supplementary Information

Table S4.1 List of invertebrate taxa observed in hull fouling assemblages of vessels arriving at the Port of Churchill, Manitoba. Frequency of occurrence in 13 vessels, mean abundance (± S.E.M.) when present, presence of live specimens (Y = yes), taxa category, and references used are also included. HB = Hudson Bay, CA = Canadian Arctic, AR = Arctic, NA = non-Arctic, and UK = unknown. Asterisks indicate taxa considered as nonindigenous to Churchill in this study.

Taxon	Occurrence (%)	Mean abundance (individuals ship^{-1})	Live specimen	Category	References
Acari					
Halacaridae	1 (7.7%)	8,907		UK	
Amphipoda					
Calliopius laeviusculus	1 (7.7%)	555	Y	HB	Steele 1961; Bousfield 1973; Stewart and Lockhart 2005
Crassicorophium bonellii	1 (7.7%)	59		AR*	Bousfield 1973; EOL 2014; Sirenko et al. 2014
Gammaracanthus loricatus	1 (7.7%)	538	Y	HB	Steele 1961; Atkinson and Wacasey 1989; Stewart and Lockhart 2005
Gammarus oceanicus	1 (7.7%)	5,731	Y	HB	Atkinson and Wacasey 1989; Stewart and Lockhart 2005; Goldsmit et al. 2014
Gammarus setosus	5 (23.1%)	5,895 ± 711		HB	Atkinson and Wacasey 1989; Stewart and Lockhart 2005; Goldsmit et al. 2014
Gammarus sp.	1 (7.7%)	187	Y	UK	
Jassa marmorata	1 (7.7%)	5		AR*	Bousfield 1973; EOL 2014; Sirenko et al. 2014

Bivalvia					
Bivalvia (juveniles)	3 (23.1%)	4,790 ± 1,797	Y	UK	
Chamidae	2 (15.4%)	3,400 ± 1,295		UK	
Corbulidae	1 (7.7%)	10		UK	
Hiatella arctica	2 (15.4%)	3,472 ± 1,326	Y	IN	Atkinson and Wacasey 1989; Stewart and Lockhart 2005; Goldsmit et al. 2014
Musculus sp.	1 (7.7%)	44		UK	
Myidae	1 (7.7%)	6,702		UK	
Mytilidae	5 (38.5%)	963 ± 513		UK	
Mytilus edulis	1 (7.7%)	198		HB	Atkinson and Wacasey 1989; Stewart and Lockhart 2005; Goldsmit et al. 2014
Mytilus sp.	2 (15.4%)	2,569 ± 996		UK	
Chironomidae				UK	
Chironomidae	1 (7.7%)	306		UK	
Cirripedia					
Amphibalanus amphitrite	5 (38.5%)	112,859 ± 69,678	Y	NA*	Newman and Ross 1976; Fofonoff et al. 2003
Amphibalanus eburneus	1 (7.7%)	530	Y	NA*	Newman and Ross 1976; Carlton et al. 2011; Fofonoff et al. 2003
Amphibalanus improvisus	3 (23.1%)	11,396 ± 3,511	Y	NA*	Henry and MacLaughlin 1975; Fofonoff et al. 2003
Amphibalanus reticulatus	3 (23.1%)	11,432 ± 5,373	Y	NA*	Newman and Ross 1976; Fofonoff et al. 2003
Amphibalanus sp. 1	1 (7.7%)	78,371		UK	
Amphibalanus sp. 2	2 (15.4%)	62		UK	
Austrominius modestus	1 (7.7%)	2,005	Y	NA*	Newman and Ross 1976; CABI 2014; OBIS 2014

Balanidae sp. 1	8 (61.5%)	130,559 ± 62,593	Y	UK	
Balanidae sp. 2	1 (7.7%)	54	Y	UK	
Balanoidea sp.	1 (7.7%)	155,563	Y	UK	
Balanus trigonus	2 (15.4%)	371,564 ± 98,584	Y	NA*	Newman and Ross 1976; CABI 2014; OBIS 2014
Conchoderma auritum	1 (7.7%)	1,074	Y	NA*	OBIS 2014
Conchoderma virgatum	1 (7.7%)	139	Y	NA*	OBIS 2014
Fistulobalanus sp.	1 (7.7%)	36,319		UK	
Megabalanus cf. *spinosus*	1 (7.7%)	10,702		NA*	Henry and MacLaughlin 1986
Megabalanus cf. *tintinnabulum*	1 (7.7%)	6,354		NA*	Darwin 1851; Pislbry 1916
Megabalanus coccopoma	2 (15.4%)	295,297 ± 115,396		NA*	Fofonoff et al. 2014
Megabalanus sp. 1	1 (7.7%)	1,882		UK	
Megabalanus sp. 2	1 (7.7%)	1,556,885		UK	
Megabalanus sp. 3	3 (23.1%)	122,012 ± 57,591		UK	
Newmanella sp.	1 (7.7%)	57,861		UK	
Perforatus sp.	2 (15.4%)	310,445 ± 121,268	Y	UK	
Cladocera					
Acantholeberis curvirostris	1 (7.7%)	2,164		NA*	EOL 2014
Alona sp.	1 (7.7%)	59			
Copepoda					
Acartia hudsonica	3 (23.1%)	5,438 ± 1,412		CA	Roff and Legendre 1986; OBIS 2014
Acartia longiremis	1 (7.7%)	139		HB	Shih et al. 1971; Roff and Legendre 1986; Stewart and Lockhart 2005
Acartia sp.	3 (23.1%)	3,240		UK	
Calanoida	4 (30.8%)	6,671 ± 2,945		UK	
Calanus finmarchicus	1 (7.7%)	36		HB	Shih et al. 1971; Grainger 1963; Roff and Legendre 1986

Calanus sp.	1 (7.7%)	3,889		UK	
Centropages sp.	1 (7.7%)	563		UK	
Cyclopoida	3 (23.1%)	560 ± 231		UK	
Dactylopusia vulgaris	1 (7.7%)	45		HB	Shih et al. 1971; Stewart and Lockhart 2005
Ectinosoma sp.	1 (7.7%)	4		UK	
Harpacticoida	1 (7.7%)	4		UK	
Harpacticus sp.	1 (7.7%)	45		UK	
Laophontidae sp.	1 (7.7%)	1,585		UK	
Mesochra sp.	1 (7.7%)	5,108		UK	
Metridia lucens	1 (7.7%)	15,323		HB	Shih et al. 1971; Stewart and Lockhart 2005
Microsetella norvegica	3 (23.1%)	3,369 ± 1,509	Y	HB	Shih et al. 1971
Oithona similis	3 (23.1%)	4,670 ± 1,562		HB	Shih et al. 1971; Roff and Legendre 1986
Oncaea sp.	1 (7.7%)	632		UK	
Paradactylopodia brevicornis	1 (7.7%)	139		CA	Shih et al. 1971
Paronychocamptus huntsmani	3 (23.1%)	11,037 ± 3,250		NA*	Shih et al. 1971; OBIS 2014; WoRMS 2014
Pseudcalanus sp.	2 (15.4%)	220 ± 77		UK	
Pseudobradya sp.	1 (7.7%)	145		UK	
Sarsamphiascus minutus	1 (7.7%)	5,118		CA	Shih et al. 1971
Schizopera clandestina?	2 (15.4%)	72 ± 23		NA*	EOL 2014; WoRMS 2014
Tisbe furcata?	1 (7.7%)	561		HB	Shih et al. 1971; Stewart and Lockhart 2005
Zaus sp.	2 (15.4%)	111 ± 11		UK	
Echinodermata					
Phoronida	1 (7.7%)	4,265		UK	

Gastropoda				
Patellogastropoda	1 (7.7%)	125	UK	
Nematoda				
Camacolaimus sp.	1 (7.7%)	4	UK	
Chromadoridae	1 (7.7%)	59	UK	
Chromadorina sp.	1 (7.7%)	10,171	UK	
Chromadorita sp.	1 (7.7%)	96	UK	
Dichromadora sp.	1 (7.7%)	19	UK	
Geomonhystera sp.	2 (15.4%)	47 ± 9	AR*	Fisher per. comm. 2009; OBIS 2014
Ironidae	1 (7.7%)	8,848	UK	
Leptolaimoides sp.	1 (7.7%)	12	UK	
Oncholaimus sp.	1 (7.7%)	12	UK	
Prochromadora orleji	1 (7.7%)	202,712	NA*	EOL 2014; OBIS 2014
Prochromadora sp.1	1 (7.7%)	40,387	UK	
Prochromadora sp.2	2 (15.4%)	6,538 ± 2,537	UK	
Ostracoda				
Cytherocopina	1 (7.7%)	1,113	UK	
Polychaeta				
Exogone sp.	1 (7.7%)	125	UK	
Phyllodoce sp.	1 (7.7%)	27	UK	
Phyllodocidae	2 (15.4%)	2,402 ± 731	UK	
Spionidae	1 (7.7%)	70	UK	

Table S4.2 List of invertebrate taxa found in ballast water of vessels arriving at the Port of Churchill, Manitoba. Frequency of occurrence in 32 vessels, mean abundance (± S.E.M.) when present, taxa category, and references used were also included. Taxa present in port water samples were considered native to Hudson Bay. Code as per Supplementary Table S4.1. Asterisks indicate taxa considered as nonindigenous to Churchill in this study.

Taxon	Occurrence (%)	Mean abundance (individuals ship^{-1})	Category	References
Acari				
Acari	2 (6.3%)	26,096 ± 3,633	UK	
Amphipoda				
Themisto gaudichaudi	7 (21.9%)	59,470 ± 7,488	CA	Shih et al. 1971; Stewart and Lockhart 2005
Themisto sp.	1 (3.1%)	9,212	UK	
Bivalvia				
Bivalvia (juveniles)	7 (21.9%)	172,524 ± 41,328	HB	Water samples
Chaetognatha				
Sagittidae	1 (3.1%)	10,753		
Cirripedia				
Cirripedia (larvae)	9 (28.1%)	632,893 ± 300,133	HB	Water samples
Cladocera				
Cladocera	1 (3.1%)	150,028		
Daphnia sp.	1 (3.1%)	19,380		
Copepoda				
Acartia clausi	3 (9.4%)	3,854,453 ± 887,656	HB	Shih et al. 1971; Roff and Legendre 1986; Stewart and Lockhart 2005
Acartia hudsonica	2 (6.3%)	40,198,578 ± 17,778,782	CA	OBIS 2014

Acartia sp.	1 (3.1%)	932,957	UK	
Calanoida	2 (6.3%)	52,396 ± 34,815	UK	
Calanus finmarchicus	1 (3.1%)	2,321,454	HB	Wiley 1931; Grainger 1963; Roff and Legendre 1986
Calanus glacialis	3 (9.4%)	8,879,446 ± 3,854,319	HB	Shih et al. 1971; Grainger 1963; Grainger 1968
Calanus sp.	2 (6.3%)	34,553	UK	
Centropages hamatus	1 (3.1%)	1,079,341	HB	Shih et al. 1971; Boxshall 2014
Centropages sp.	1 (3.1%)	1,892,957	UK	
Centropages typicus	1 (3.1%)	524,587	AR*	Shih et al. 1971; OBIS 2014
Clausocalanus mastigophorus	2 (6.3%)	306,293 ± 38,702	HB	Shih et al. 1971; Stewart and Lockhart 2005
Copepoda	2 (6.3%)	9,217 ± 848	UK	
Cyclopoida	1 (3.1%)	34,176	UK	
Ectinosoma sp.	1 (3.1%)	8,830	UK	
Euterpina acutifrons	2 (6.3%)	1,499,803 ± 11,958	CA	OBIS 2014
Heterolaophonte ströemi	1 (3.1%)	22,891	AR*	Shih et al. 1971; Kotwicki 2002
Metridia lucens	1 (3.1%)	208,188	HB	Shih et al. 1971; Stewart and Lockhart 2005
Microsetella norvegica	12 (37.5%)	630,804 ± 138,881	HB	Water samples; Shih et al. 1971
Nitokra lacustris	1 (3.1%)	739,393	NA*	Rhodes 2003; WoRMS 2014
Oithona atlantica	1 (3.1%)	14,935,778	CA	WoRMS 2014
Oithona similis	23 (71.9%)	11,351,661 ± 3,678,529	HB	Water samples; Shih et al. 1971; Roff and Legendre 1986
Oncaea sp.	8 (25.0%)	407,633 ± 197,929	UK	
Paracalanus parvus	5 (15.6%)	4,373,285 ± 1,105,744	HB	Shih et al. 1971
Pseudocalanus newmani	3 (9.4%)	690,386 ± 124,622	CA	Stewart and Lockhart 2005
Pseudocalanus sp.	2 (6.3%)	418,046 ± 140,494	UK	
Temora longicornis	2 (6.3%)	5,180,515 ± 995,940	CA	Shih et al. 1971

Tisbe furcata?	1 (3.1%)	25,632	HB	Water samples; Shih et al. 1971; Stewart and Lockhart 2005
Echinodermata				
Echinodermata	1 (3.1%)	9,309	UK	
Ophiuroidea	1 (3.1%)	133,590	UK	
Gastropoda				
Calyptraeidae	3 (9.4%)	34,686 ± 3,759	UK	
Cerithiidae	1 (3.1%)	19,710	UK	
Gastropoda	2 (6.3%)	12,156 ± 712	UK	
Heterobranchia	5 (15.6%)	1,679,009 ± 439,589	UK	
Rissoidae	1 (3.1%)	8,700	UK	
Isopoda				
Gnathiidae	2 (6.3%)	30,464 ± 5,524	UK	
Nematoda				
Ascolaimus sp.	1 (3.1%)	67,830	AR*	Fisher per. comm. 2009; EOL 2014; OBIS 2014
Axonolaimidae	1 (3.1%)	78,840	AR*	Fisher per. comm. 2009; EOL 2014; Sirenko et al. 2014
Chromadoridae	2 (6.3%)	32,760 ± 1,665	UK	
Comesomatidae	1 (3.1%)	13,366	UK	
Daptonema tenuispiculum	2 (6.3%)	159,270 ± 3,682	NA*	OBIS 2014
Geomonhystera sp.	4 (12.5%)	189,361 ± 22,165	AR*	Fisher per. comm. 2009; OBIS 2014
Omicronema sp.	1 (3.1%)	42,720	UK	
Prochromadora sp.	4 (12.5%)	81,436 ± 8,835	UK	
Polychaeta				
Hesionidae	1 (3.1%)	12,795	UK	
Pholoididae	1 (3.1%)	27,927	UK	
Polydora sp.	2 (6.3%)	62,465 ± 11,266	UK	
Spionidae	5 (15.6%)	204,804 ± 58,053	UK	

Streblospio sp.	1 (3.1%)	129,035	UK	
Rotifera				
Rotifera	4 (12.5%)	16,893 ± 725	UK	
Synchaetidae	4 (12.5%)	23,108,818 ± 8,149,955	HB	Water samples

Table S4.3 A list of references used to determine the invasion status of taxa identified in hull fouling and ballast water assemblages of vessels arriving at the Port of Churchill.

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CHAPTER 5: ASSESSING INTRODUCTION RISK USING SPECIES' RANK-ABUNDANCE DISTRIBUTIONS[4]

5.1 Introduction

Ecologists have long been interested in the structure of biological communities, namely the species abundance distribution or relative abundance of all species recorded in an area (e.g. McGill et al. 2007). Species abundance distributions have been studied extensively in natural systems to test models of community assembly including the unified neutral theory of biodiversity and biogeography (Hubbell 2001), to compare multiple communities along environmental gradients (MacNally 2007), to monitor communities across time (Thibault et al. 2004), and to identify rare species for conservation (Dunstan et al. 2012). Frequently, species abundance distribution data are visualized in rank-abundance distributions by plotting log-abundance versus species rank (e.g. Preston 1948; Dunstan et al. 2012). Rank-abundance distributions have been widely used in various sub-disciplines of ecology, but rarely in invasion ecology (Briski et al. 2014; Drake et al. 2014).

Large, mixed-species assemblages are often unintentionally introduced into areas beyond their natural range by invasion vectors such as ships' ballast water or fouled hulls (Sylvester et al. 2011), bait worm packaging (Haska et al. 2012), straw and hay (Conn et al. 2010), and wood dunnage (Haack et al. 2014), resulting in introduction of nonindigenous species (NIS). An introduction event involving a mixed-species

[4] Chan FT, Bradie J, Briski E, Bailey SA, Simard N, MacIsaac HJ. Assessing introduction risk using species' rank-abundance distributions. Proceedings of the Royal Society B (in revision)

assemblage begins with a vector that entrains individuals, often randomly, from a source community. If a sufficiently large number of individuals are entrained, most or all species in the source community may be represented within the transport vector (Lockwood et al. 2009). Generally, only a portion of entrained individuals survive transportation and are released into a new environment, resulting in attenuation of entrained individuals and/or species (e.g. Coutts et al. 2010; Brisk et al. 2013). Vector management efforts such as open-ocean ballast water exchange (BWE) and phytosanitory treatment of wood dunnage further reduce the number of entrained individuals (Bailey et al. 2011; Haack et al. 2014). Therefore, the structure of the entrained assemblage may vary sharply from that in the source community as it transitions through the transportation phase prior to release. Analysing how characteristics of an entrained assemblage vary over time during transport may provide insights into how introduction risk changes before propagules are released.

Invasion ecologists often focus on the number of transported species (i.e. colonization pressure [CP]) and their respective abundances (i.e. propagule pressure [PP] of individual species or of the entire taxonomic group [total PP]) when characterizing species assemblages transported by vectors (e.g. Conn et al. 2010; Haska et al. 2012; Briski et al. 2013). Theoretical and empirical studies have demonstrated a positive relationship between PP of a species and its probability of establishment (e.g. Colautti al. 2006; Simberloff 2009; Bradie et al. 2013). For a single introduction event, large PP reduces the likelihood of demographic stochasticity and Allee effects (Simberloff 2009). Similarly, greater CP also increases invasion risk by increasing the probability that at least one species will tolerate the new environment and form a reproducing population (Lockwood et al 2009). Recently, researchers have begun to explore relationships

between CP and PP for species assemblages entrained by vectors (Lockwood et al 2009; Briski et al. 2012; Chan et al. 2014; Chapter 3). If species introduction is a random sampling process, CP should be positively related to PP because larger inocula are expected to include more species than smaller ones (Lockwood et al. 2009).

While CP and PP are important parameters for characterizing introduction risk, they provide no information regarding the structure of the entrained assemblage. Given the stochastic nature of the entrainment process, many assemblage structures are plausible, ranging from those with highly variable abundances across species (i.e. uneven assemblages with steep rank-abundance gradients) to those with relatively equal abundances (i.e. shallow rank-abundance gradients) (Drake et al. 2014). The case of uneven assemblage structure is of special concern because both mean abundance per species (mean PP) and total PP fail to describe the variation in abundances across species (Drake et al. 2014). These measures may underestimate population size of dominant species and overestimate that of rare ones (Drake et al. 2014). Given the strong ecological consequence of biased estimates, Drake et al. (2014) argued that rank-abundance distribution be considered in addition to CP and PP when characterizing risk associated with mixed-species assemblages in invasion vectors.

Briski et al.'s (2014) conceptual model characterizing community dynamics in ballast water during transportation has not been tested empirically using repeated measurements during voyages, nor does it consider the effect of biogeographic source region or BWE. In this study, I examined changes in assemblage structure of different taxa (invertebrates, diatoms, and dinoflagellates) in control and exchanged ballast water during trans-Atlantic and trans-Pacific voyages to Canada. I use rank-abundance

distributions in transported assemblages to test three hypotheses: changes in assemblage structure and CP:total PP during transportation are the same for i) different voyage routes or ii) different taxonomic groups or iii) in response to BWE.

5.2 Methods and Materials

Plankton datasets

To analyse temporal variation in CP and total PP, I examine three datasets representing 16 invertebrate, 12 diatom, and eight dinoflagellate assemblages collected from ballast water during two trans-Atlantic and two trans-Pacific voyages, hereafter referred to as 'Atlantic' and 'Pacific', respectively (Table 5.1). Datasets were selected on the basis of common methodologies and taxonomic resolution to the species level. Methods for sample collection, enumeration, and identification are detailed elsewhere (DiBacco et al. 2007a, 2012; Klein et al. 2010; Simard et al. 2011). For Atlantic voyages, eight tanks were repeatedly sampled for each taxonomic group at different time points (i.e. eight assemblages for each group). Only invertebrate and diatom data were available for Pacific voyages. For Pacific voyage 1, invertebrate and diatom samples were collected by repeatedly sampling four tanks at different time points. During Pacific voyage 2, four tanks were sampled for invertebrates only. As a result, eight invertebrate and four diatom assemblages were surveyed during Pacific voyages. For both Atlantic and Pacific voyages, half of tanks underwent BWE using the empty-refill method, hereafter referred to as 'exchanged tanks'. Remaining tanks served as controls, hereafter 'control tanks'. I compiled a database recording the number and identity of all species, total abundance of each species, sampling time point, and date of BWE, if conducted, for

each plankton assemblage. I excluded individuals that were not identified to species level because they could obscure the relationship between CP and total PP; approximately 70-95% of the data in each dataset was retained for analyses.

Rank-abundance distributions and CP:total PP curves

For each plankton assemblage, I constructed a series of rank-abundance distributions at different time points during the transoceanic voyage. I then generated corresponding CP:total PP curves for each rank-abundance distribution using Monte Carlo simulations in R version 3.0.2 (R Development Core Team 2013). Individuals were randomly selected from the empirical distribution, without replacement, with a sample size ranging from 1 to 2,500 (total N). One thousand iterations were conducted at each sample size, following which mean number of species (i.e. mean CP) was determined for each total PP. In addition, I estimated asymptotic species richness for each assemblage at different time points using the Chao-1 estimator in SPADE version 2012/Oct 23 to account for under-sampling (Chao and Shen 2010). While rank-abundance distributions and CP:total PP curves were estimated for each sampling day, I present results for only five days for brevity, corresponding with the beginning, middle (particularly the last and first available time point immediately before and after BWE, respectively, in exchanged tanks), and end of voyages.

Using models proposed by Lockwood et al. (2009), Briski et al. (2014), and Drake et al. (2014) as foundations, I developed a conceptual model describing four relative introduction risk scenarios: high risk: high CP and high total PP; moderate risk: high CP and low total PP or low CP and high total PP; and low risk: low CP and low total PP

(Figure 5.1a). I overlaid final CP and total PP values for the last sampling point on my model to estimate relative introduction risk among transported assemblages. Furthermore, I used the t-test to test for differences in final CP (and total PP) between Atlantic and Pacific voyages, and between exchanged and control tanks for each taxonomic group within each voyage route. Comparisons were limited to those of the same taxonomic group to avoid biases due to differences in collection methods and life history traits. In addition, all comparisons were made in relative terms, assuming uniform establishment probabilities and environmental suitability among transported species. I characterized total PP rather than mean PP because the partitioning of total abundance evenly across all species makes it impossible to obtain high CP and total PP scenarios. My analysis estimates introduction risk per ballast sample. To estimate introduction risk for an individual vessel, one must multiply total PP and CP by the total ballast discharge volume.

Statistical analyses

I applied three broad analytical approaches using linear mixed-effects models to investigate patterns observed in rank-abundance distributions and CP:total PP curves for each taxonomic group. Linear mixed-effects models are appropriate in this context because the datasets have hierarchical structure, in which ballast tanks are nested within ships and repeated measurements are collected from individual tanks (see Zuur et al. 2009). I used the observed CP rather than estimated species richness in these analyses because the number of singletons and doubletons (i.e. species represented by only one and two individuals, respectively) increased with time as the abundance of most species

decreased, inflating the number of rare species and thus overestimating complete species richness. First, I constructed separate models to test the effect of time on CP and total PP using data collected from control tanks. I treated time (i.e. days since uptake of ballast water) and quadratic variant of time ($time^2$) as fixed explanatory variables. Twelve models (two response variables [CP and total PP] × three taxonomic groups × two voyage routes) were constructed for this step of the analyses. Secondly, to test the effect of voyage route (Atlantic vs. Pacific) on CP and total PP, I treated time, $time^2$, voyage route, and the interaction between time and voyage (time × voyage) as fixed explanatory variables in four separate models (two each for invertebrates and diatoms). To distinguish the effects of biogeographic region and voyage length, I constructed four follow-up models using the same fixed explanatory variables and included only the first nine days so that both routes encompassed the same voyage length, allowing examination of the importance of route.

Finally, I constructed a series of models to test the effect of BWE on CP and total PP for each taxonomic group using data from both control and exchanged tanks. As a first step, I built six separate models (two response variables × three taxonomic groups) to determine if there were inherent differences in CP and total PP between control and exchanged tanks prior to BWE. I included time, $time^2$, voyage route, BWE status, time × voyage route, as well as the interactions between time and BWE status (time × BWE status), and between BWE status and voyage route (BWE status × voyage route) as fixed explanatory variables. Here, time was defined as the number of days between ballast water uptake and BWE. Measurements collected after BWE were excluded in these analyses. Results of the models suggested that BWE status was not related to CP and total

PP in all models (results not presented). Therefore, I concluded there were no inherent differences in CP and total PP between treatment tanks prior to BWE. Next, I fitted six separate models (two response variables × three taxonomic groups) to test the effect of BWE on CP and total PP. I included time, time^2, voyage route, BWE status, time × voyage route, time × BWE status, and voyage route × BWE status as fixed explanatory variables. Here I defined time as the number of days after BWE. To investigate the effects of time × voyage route and voyage route × BWE status on CP and total PP, I constructed four follow-up models (two each for invertebrates and diatoms) with time, time^2, BWE status, and time × BWE status as fixed explanatory variables.

I included tank and ship as hierarchical grouping variables in all models to accommodate the nested nature of the datasets. In addition, I specified a simple autoregressive covariance structure for the models to account for temporal autocorrelation between repeated measurements (Cnaan et al. 1997). I applied the top-down strategy to identify optimal models having both fixed and random effects beginning with three beyond-optimal models containing all explanatory variables and their interactions but different random components: i) no random terms except for ordinary residuals; ii) a random intercept model; and iii) a random intercept and slope model (Zuur et al. 2009). I assessed random components by comparing Akaike Information Criterion values estimated using restricted maximum likelihood estimation. Once the optimal random structure was found, I identified the optimal fixed structure by conducting sequential t-tests using restricted maximum likelihood estimation. Non-significant fixed effects were removed in a stepwise manner until minimum adequate models containing only significant factors remained. I used visual inspection of model residuals to check for

a normal distribution and homogeneity of variance. All analyses were conducted using the *lme* and *gls* functions in R. The latter function was used on models lacking random effects (Zuur et al. 2009).

I compared results obtained from rank-abundance distributions with those from more traditional analyses of total and mean PP, in order to examine differences in the methodologies.

5.3 Results

Rank-abundance distributions and CP:total PP curves varied temporally across voyage routes and taxonomic groups (Table 5.2, Figure 5.2, and Supplementary Figures S5.1-5.4). For Atlantic voyages, no changes in CP but significant attenuation of total PP were observed for invertebrates (Table 5.2a, Figure 5.2, and Supplementary Figure S5.1); the opposite pattern was noted for diatoms (Table 5.2a, Figure 5.2, and Supplementary Figure S5.3). CP for dinoflagellates decreased significantly over time in a quadratic trend (i.e. greater than linear decline over time), whereas total PP remained unchanged (Table 5.2a, Figure 5.2, and Supplementary Figure S5.4). Reductions in total PP for invertebrates and dinoflagellates were attributed to decreases in abundance of mainly moderately common species and a few rare species, whereas losses in total PP for diatoms resulted from uniform decreases in abundance across all species (Figure 5.2 and Supplementary Figures S5.1, S5.3, and S5.4). As a result, rank-abundance gradients were steeper over time for invertebrates and dinoflagellates, and gentler for diatoms (Figure 5.22 and Supplementary Figures S5.1, S5.3, and S5.4).

For Pacific voyages, both CP and total PP decreased significantly for invertebrates as a quadratic function of time (Table 5.2a), the latter due to decreases in abundance of

moderately common and rare species, though dominant species also suffered high mortality (Figure 5.2 and Supplementary Figure S5.2). In contrast, diatoms exhibited significantly greater than linear reduction in CP but no changes in total PP (Table 5.2a, Figure 5.2, and Supplementary Figure S5.3). Rank-abundance distributions for both groups had increasingly steep gradients over time (Figure 5.2 and Supplementary Figures S5.2 and S5.3).

Changes in rank-abundance distributions and CP:total PP were generally less apparent for the Atlantic than for the Pacific voyages (Figure 5.2 and Supplementary Figures S5.1-5.4). CP for invertebrates was significantly affected by voyage route, with lower CP observed for Atlantic than Pacific (Table 5.2b). However, CP declined at a slower rate for the Atlantic than the Pacific as indicated by the significant interaction between time and voyage route (i.e. different regression slopes; Table 5.2b). There were no differences in total PP for invertebrates between voyage routes, but it decreased at a slower rate for Atlantic than Pacific voyages (significant time × voyage route interaction; Table 5.2b). CP for diatoms decreased significantly over time but it did not vary by voyage routes, whereas total PP did not vary over time but was significantly higher for Atlantic than Pacific voyages (Table 5.2b). I could not compare the effect of voyage route for dinoflagellates, as only Atlantic route data were available.

If analysis was limited to the first nine days of voyages, CP for invertebrates did not change over time, but was significantly lower for Atlantic than Pacific voyages (Table 5.2c). Conversely, total PP for invertebrates decreased significantly over time but was not associated with voyage route (Table 5.2c). Both CP and total PP of diatoms were

predicted by the same explanatory variables as the full models, except that the former changed in a linear rather than quadratic trend (Table 5.2c).

Visual comparison of rank-abundance distributions and CP:total PP at the last sampling point prior to BWE versus those at the last sampling point near the end of the voyage in exchanged tanks suggest that the effect of BWE varied across voyage routes and taxonomic groups (Figure 5.3 and Supplementary Figures S5.5-5.8). For Atlantic routes, there were few changes in CP for invertebrates and moderate attenuation of total PP after BWE owing to reductions in population abundance of moderately common and rare species; rank-abundance gradients were similar before and after BWE (Figure 5.3 and Supplementary Figure S5.5). Changes in CP after BWE varied from relatively strong reductions to slight increases in CP, accompanied by relatively moderate to strong attenuation of total PP for diatoms; rank-abundance gradients remained relatively shallow owing to uniform reductions in population abundance of all species or additions of new species at low abundance (Figure 5.3 and Supplementary Figure S5.7). Similarly, I noted strong increases in CP for dinoflagellates owing to addition of new species at low abundances and marked reductions in total PP due to decreases in abundance of dominant species after BWE; rank-abundance gradients were generally more even post-BWE (Figure 5.3 and Supplementary Figure S5.8).

For Pacific routes, responses in CP for invertebrates ranged from relatively moderate reductions to mild increases owing to either losses or gains of rare species, whereas total PP consistently increased due to higher population abundances of dominant species after BWE; rank-abundance gradients were typically steeper after BWE (Figure 5.3 and Supplementary Figure S5.6). While I observed relatively mild increases in CP

due to additions of rare diatom species, changes in total PP varied from relatively moderate reductions to strong increases in total PP owing to increased abundance of dominant species; rank-abundance gradients were steeper after BWE in some but not all cases (Figure 5.3 and Supplementary Figure S5.7).

Comparisons of CP and total PP between exchanged and control tanks further indicate that the effect of BWE varied across voyage routes and taxonomic groups (Table 5.3). CP for invertebrates was significantly associated with time, voyage route, and their interaction (i.e. the effect of time varied between voyage routes) as well as BWE status (Tables 5.3). CP for invertebrates was higher in both exchanged and control tanks for Atlantic than Pacific routes; however, CP decreased over time for the Atlantic, whereas it increased over time for the Pacific (Tables 5.3 and Supplementary Table S5.1). When comparing between exchanged and control tanks, CP for invertebrates was significantly higher in exchanged than in control tanks for both voyage routes (Table 5.3 and Supplementary Table S5.1). Total PP for invertebrates was significantly associated with voyage route as well as the interactions between time and voyage route, and BWE status and voyage route (i.e. the effect of BWE varied between locations; Table 5.3). Total PP for invertebrates was higher in all tanks for Atlantic than Pacific voyages. While total PP for invertebrates decreased over time for Atlantic voyages, it did not change for Pacific ones (Tables 5.3 and Supplementary Table S5.1). There were significantly lower total PP for invertebrates in exchanged than control tanks for Atlantic voyages, whereas no differences were observed for Pacific routes (Table 5.3 and Supplementary Table S5.1). For diatoms, there were no predictors of CP, likely due to high variation observed across assemblages and small sample size (n = 6) (Table 5.3; see also Figure 5.3 and

Supplementary Figure S5.7). Total PP for diatoms was significantly associated with the interaction between BWE status and voyage route (Table 5.3). Total PP for diatoms was lower in exchanged than control tanks for Atlantic voyages, however there were no differences in total PP between treatments for Pacific ones (Table 5.3 and Supplementary Table S5.1). Finally, for dinoflagellates, BWE status was a predictor of CP, which surprisingly was significantly higher in exchanged than control tanks (Table 5.3). In contrast, there were no differences in total PP for dinoflagellates between treatments (Table 5.3).

Final CP and total PP for Atlantic routes were significantly higher than those for Pacific ones (t-test, $p < 0.01$ in both cases), suggesting that the former presented a higher introduction risk (Figure 5.1b). For Atlantic routes, significantly higher final CP but lower total PP were observed for invertebrates in exchanged tanks when compared to those in control tanks (t-test, $p = 0.01$ and $p = 0.02$, respectively), thus introduction risk did not appear to change following BWE (Figure 5.1b). There were no significant differences in final CP and total PP for diatoms between exchanged and control tanks (t-test, $p = 0.63$ and $p = 0.13$, respectively), indicating no apparent differences in introduction risk between treatments (Figure 5.1b). Conversely, dinoflagellates in exchanged tanks exhibited significantly higher final CP but no differences in total PP relative to those in control tanks (t-test, $p = 0.02$ and $p = 0.26$, respectively), thereby posing a higher introduction risk (Figure 5.1b). For Pacific voyages, invertebrates from exchanged tanks demonstrated significantly higher final CP but no differences in total PP when compared to those from control ones (t-test, $p < 0.01$ and $p = 0.11$, respectively), suggesting that the taxonomic group posed a greater introduction risk post-BWE (Figure

5.1b). I could not compare final CP and total PP for diatoms between exchanged and control tanks for statistical differences owing to insufficient sample size. However, Figure 5.1b suggests that diatoms from exchanged tanks exhibited higher final CP and similar total PP when compared to those from control ones, thereby potentially posing higher introduction risk.

My comparison of rank-abundance distributions to more traditional summary methods indicated that total PP was strongly influenced by the most dominant species, and did not provide any information regarding abundances of moderately common or rare species (Figures 5.2-5.3 and Supplementary Figures S5.1-5.8). Mean PP (± S.E.M) summarized variation in abundances among species, with greater variation associated with more uneven assemblages, though it typically underestimated abundance of dominant species while greatly overestimating that of rare ones (Figures 5.2-5.3 and Supplementary Figures S5.1-S5.8).

5.4 Discussion

Understanding the dynamics of a species assemblage during the transport stage prior to introduction can provide insights into how invasion risk changes temporally (Briski et al. 2014; Drake et al. 2014). Characterization of assemblages in invasion vectors has typically relied on CP and total PP (e.g. Conn et al. 2010; Haska et al. 2012; Briski et al. 2013). Here, I extended this approach to examine rank-abundance distributions and CP:total PP relationships for a variety of common taxa found in ships' ballast water, and to explore the importance of voyage route and BWE. My results suggest that rank-abundance distributions and CP:total PP in control tanks vary greatly by voyage route (Atlantic vs. Pacific). Responses in rank-abundance distributions and

CP:total PP for control tanks also differed by taxonomic group. Paradoxically, in certain cases BWE actually increased CP and/or total PP by adding new species or increasing the abundance of existing dominant species, thereby increasing overall introduction risk. My study thus provides a useful application of rank-abundance distributions in invasion ecology to characterize assemblages transported by vectors and to examine efficacy of management strategies.

Differences in source inocula and voyage length can both influence responses in assemblage structure during transport. When voyage length was standardized for Atlantic and Pacific trips, route significantly predicted CP or total PP, depending on the taxonomic group. It is apparent that initial rank-abundance distributions differed between Atlantic and Pacific routes within a particular taxonomic group. The effect of source region on richness and abundance of ballast water organisms has been reported previously (e.g. Verling et al. 2005; Cordell et al. 2009; Briski et al. 2013). When full voyages were considered, voyage route again was a significant predictor of CP or total PP. Furthermore, CP and/or total PP declined at faster rates during Pacific than Atlantic voyages, suggesting that trip length was also important. Overall, I observed stronger reductions in CP and/or total PP in control tanks for Pacific than Atlantic routes. Long transit times prolong organisms' exposure to biotic and abiotic stressors such as food limitation, predation, change in water temperature, and light and oxygen limitation in ballast water (Gollasch et al. 2000b; Cordell et al. 2009). Therefore, longer trips are generally associated with lower species richness and abundance of ballast water organisms (Briski et al. 2013; Chan et al. 2014).

Differences between the two voyage routes are also reflected in final CP:total PP, in which CP and total PP were typically higher for Atlantic voyages than for Pacific ones in both control and exchanged tanks. All things being equal (e.g. shipping traffic, environmental suitability, and study effort), my results suggest that vessels arriving with ballast to the Atlantic coast of Canada present a higher risk of ballast-mediated introductions. This finding is consistent with the occurrence of more nonindigenous species on the Atlantic than the Pacific coast (i.e. 112 versus 94) (Casas-Monroy et al. 2014).

Relative dynamics for CP and total PP among taxonomic groups may be attributed to taxon-specific tolerance to abiotic and biotic stresses. I observed significant attenuation of total PP, or both CP and total PP in some cases, for invertebrates. Conversely, diatoms and dinoflagellates exhibited significant reductions in CP but no changes in total PP. These findings suggest that invertebrate species generally have broad tolerance, though members of moderately common species exhibited the highest mortality. In contrast, tolerance varies by species for diatoms and dinoflagellates, in which mortality was selectively high for rare species, while moderately common and dominant species mostly survived or even reproduced during transportation (Simard et al. 2011; Klein et al. 2010). My results corroborate those described by Briski et al.'s (2014) conceptual model, with a few exceptions. Cases that deviated from the conceptual model were mostly limited to Pacific voyages, further supporting my previous findings of the effect of voyage route on assemblage dynamics.

BWE appeared to increase introduction risk in certain cases by augmenting existing populations and/or adding new species. I observed elevated risk for both invertebrates

and diatoms after BWE on Pacific voyages, the former owing to increased total PP and the latter to increased CP. Conversely, only dinoflagellates demonstrated elevated risk as a result of increased CP following BWE on Atlantic voyages. Increases in total PP but not CP following BWE indicate increased population abundance for species already present in ballast water tanks, possibly as a result of hatching from diapausing eggs promoted by loading of 'fresh' oceanic water (Bailey et al. 2003) and/or uptake of individuals of existing species during BWE (Choi et al. 2005). I attribute increases in CP after BWE to uptake of new species during BWE (see Klein et al. 2010; Simard et al 2011). My findings accord with previous studies that reported increased species richness due to the addition of new species and persistence of original ones following BWE (Taylor et al. 2007; Cordell et al. 2009; Roy et al. 2012).

Rank-abundance distributions provide a more accurate description of entrained assemblages than summary statistics including total and mean PP. My study demonstrated that rank-abundance distributions effectively characterized variation in abundance across species, making it possible to visualize and examine assemblage dynamics (e.g. changes in abundance of particular species) over time, particularly before and after vector management, thereby allowing refined estimation of introduction risk. Conversely, total or mean PP consistently over- and/or underestimated abundances of most species because entrained assemblages were generally uneven, with extent of unevenness depending on voyage route, taxonomic group, and vector management strategy. Over- and under-estimation of abundances can have strong ecological consequences, with the former leading to misidentification of high-risk introduction event (i.e. false positive), and the latter failure to recognize one (i.e. false negative).

Characterizing assemblage dynamics during transport and identifying factors that influence changes can improve our ability to forecast future invasions. I am not aware of studies on temporal changes in assemblage structure during transport in vectors other than ballast water. I propose that the use of rank-abundance distributions – a tool commonly used to characterize communities in natural habitats – and the analysis of CP and total PP relationship be extended to assemblages entrained by the myriad of invasion vectors. Rank-abundance distributions, CP:total PP relationship, and introduction risk may vary among vectors. For example, biofouling communities on a ship's hull are exposed to very hostile transport conditions (i.e. high selection pressure) due to shear stresses and changing environmental conditions (Sylvester et al. 2011), thus introduction risk likely changes over time. In contrast, species assemblages associated with live algae used as bait worm packaging should be exposed to low selection pressures during transport because environmental conditions are optimized to prevent loss of bait worms (Haska et al. 2011), thus I expect little to no change in introduction risk. In addition, factors including geographic route and vector management strategies may further affect the dynamics of an entrained assemblage, thus influencing introduction risk.

Table 5.1 Plankton datasets used in this study including data source, voyage route (Atlantic vs. Pacific), origin of ballast water, destination port, duration, taxonomic group (invertebrates, diatoms, and dinoflagellates), ballast water exchange (BWE) status (Y, yes; N, no), and number of sampled tanks.

Voyage route	Origin of ballast water	Destination port	Duration (days)	Taxonomic group	BWE (Y/N)	No. of sampled tanks	Data source
Atlantic 1	Rotterdam, Netherlands	Sept-Îles, Canada	7	Invertebrates	Y	2	Simard et al. 2011
					N	2	
				Diatoms	Y	2	Simard et al. 2011
					N	2	
				Dinoflagellates	Y	2	Simard et al. 2011
					N	2	
Atlantic 2	Rotterdam, Netherlands	Sept-Îles, Canada	9	Invertebrates	Y	2	Simard et al. 2011
					N	2	
				Diatoms	Y	2	Simard et al. 2011
					N	2	
				Dinoflagellates	Y	2	Simard et al. 2011
					N	2	
Pacific 1	Hakata, Japan	Vancouver, Canada	24	Invertebrates	Y	2	DiBacco 2007
					N	2	
Pacific 2	Osaka, Japan	Vancouver, Canada	23	Invertebrates	Y	2	DiBacco 2007
					N	2	
Pacific 1	Hakata, Japan	Vancouver, Canada	24	Diatoms	Y	2	Klein et al. 2010
					N	2	

Table 5.2 Results of linear mixed-effects models testing the fixed effects of (a) time and quadratic term of time (time^2) and (b) time, time^2, voyage route, and the interaction term between time and voyage route (time × voyage route) for colonization pressure and total propagule pressure associated with invertebrate and diatom assemblages in control tanks during trans-Atlantic and trans-Pacific voyages separately and pooled together, respectively. Follow-up models (c) were conducted to distinguish the effects of biogeographic region and voyage length associated with voyage route. These additional models standardized voyage length for Pacific and Atlantic route to the first nine days only. Time and time^2 were included as fixed effects in (a) models for dinoflagellates. Dashes (-) indicate non-significant variables that were removed from the final optimal models.

	Invertebrates				**Diatoms**				**Dinoflagellates**			
	d.f.	β	t	p	d.f.	β	t	p	d.f.	β	t	p
(a) Colonization pressure (Atlantic)												
Time	-	-	-	-	23	-0.7	-2.9	<0.01	-	-	-	-
Time^2	-	-	-	-	-	-	-	-	20	-0.2	-3.8	<0.01
Total propagule pressure (Atlantic)												
Time	27	-5778.6	-3.3	<0.01	-	-	-	-	-	-	-	-
Time^2	-	-	-	-	-	-	-	-	-	-	-	-
Colonization pressure (Pacific)												
Time	23	-3.4	-3.4	<0.01	24	-1.3	-4.7	<0.01	n.a.	n.a.	n.a.	n.a.
Time^2	23	0.1	2.3	0.03	24	0.1	3.7	<0.01	n.a.	n.a.	n.a.	n.a.
Total propagule pressure (Pacific)												
Time	23	-23825.3	-4.7	<0.01	-	-	-	-	n.a.	n.a.	n.a.	n.a.
Time^2	23	1119.0	3.9	<0.01	-	-	-	-	n.a.	n.a.	n.a.	n.a.
(b) Colonization pressure (full voyages)												
Time	50	-3.1	-4.6	<0.01	44	-1.1	-4.8	<0.01	n.a.	n.a.	n.a.	n.a.

Time^2	50	0.11	3.0	<0.01	44	0.03	3.5	<0.01	n.a.	n.a.	n.a.	n.a.
Voyage route	50	-13.8	-5.9	<0.01	-	-	-		n.a.	n.a.	n.a.	n.a.
Time × voyage route	50	1.9	4.9	<0.01	-	-	-		n.a.	n.a.	n.a.	n.a.
Total propagule pressure (full voyages)												
Time	50	-23901.3	-5.0	<0.01	-	-	-	-	n.a.	n.a.	n.a.	n.a.
Time^2	50	1107.23	4.2	<0.01	-	-	-	-	n.a.	n.a.	n.a.	n.a.
Voyage route	-	-	-	-	50	37752.9	5.0	<0.01	n.a.	n.a.	n.a.	n.a.
Time × voyage route	50	6489.2	2.4	0.02	-	-	-	-	n.a.	n.a.	n.a.	n.a.
(c) Colonization pressure (first 9 days)												
Time	-	-	-		31	-0.8	-4.5	<0.01	n.a.	n.a.	n.a.	n.a.
Time^2	-	-	-		-	-	-		n.a.	n.a.	n.a.	n.a.
Voyage route	2	-7.1	-5.8	0.03	-	-	-		n.a.	n.a.	n.a.	n.a.
Time × voyage route	-	-	-		-	-	-		n.a.	n.a.	n.a.	n.a.
Total propagule pressure (first 9 days)												
Time	41	-32839.7	-4.6	<0.01	-	-	-	-	n.a.	n.a.	n.a.	n.a.
Time^2	41	2295.5	2.8	<0.01	-	-	-		n.a.	n.a.	n.a.	n.a.
Voyage route	-	-	-	-	35	29853.6	2.8	<0.01	n.a.	n.a.	n.a.	n.a.
Time x voyage route	-	-	-		-	-	-	-	n.a.	n.a.	n.a.	n.a.

Table 5.3 Results of linear mixed-effects models testing the fixed effects of time, time^2, voyage route, ballast water exchange (BWE) status, time × voyage route, and the interaction terms between time and BWE status (time × BWE status) and between BWE status and voyage route (BWE status × voyage route) for colonization pressure and total propagule pressure associated with invertebrate and diatom assemblages in control and BWE tanks during trans-Atlantic and trans-Pacific voyages after BWE. Time, time^2, and BWE status were included as fixed effects in models for dinoflagellates. Time was defined as the number of days since BWE. Time^2 and time × BWE status were not retained in any model. Dashes (-) indicate non-significant variables that were excluded in the final optimal models.

	Invertebrates				**Diatoms**				**Dinoflagellates**			
	d.f.	β	t	p	d.f.	β	t	p	d.f.	β	t	p
Colonization pressure												
Time	57	1.3	6.1	<0.01	-	-	-	-	-	-	-	-
Voyage route	57	6.3	12.1	<0.01	-	-	-	-	n.a.	n.a.	n.a.	n.a.
BWE status	57	1.9	6.5	<0.01	-	-	-		5	7.7	4.2	<0.01
Time × voyage route	57	-1.5	-6.5	<0.01	-	-	-	-	n.a.	n.a.	n.a.	n.a.
BWE status × voyage route	-	-	-	-	-	-	-	-	n.a.	n.a.	n.a.	n.a.
Total propagule pressure												
Time	-	-	-		-	-	-	-	31	-3255.7	-3.1	<0.01
Voyage route	56	56562.9	12.3	<0.01	-	-	-	-	n.a.	n.a.	n.a.	n.a.
BWE status	-	-	-	-	-	-	-	-	5	7.7	4.2	<0.01
Time × voyage route	56	-2093.2	-3.2	<0.01	-	-	-	-	n.a.	n.a.	n.a.	n.a.
BWE status × voyage route	56	-25323.3	-8.7	<0.01	6	33191.8	5.8	<0.01	n.a.	n.a.	n.a.	n.a.

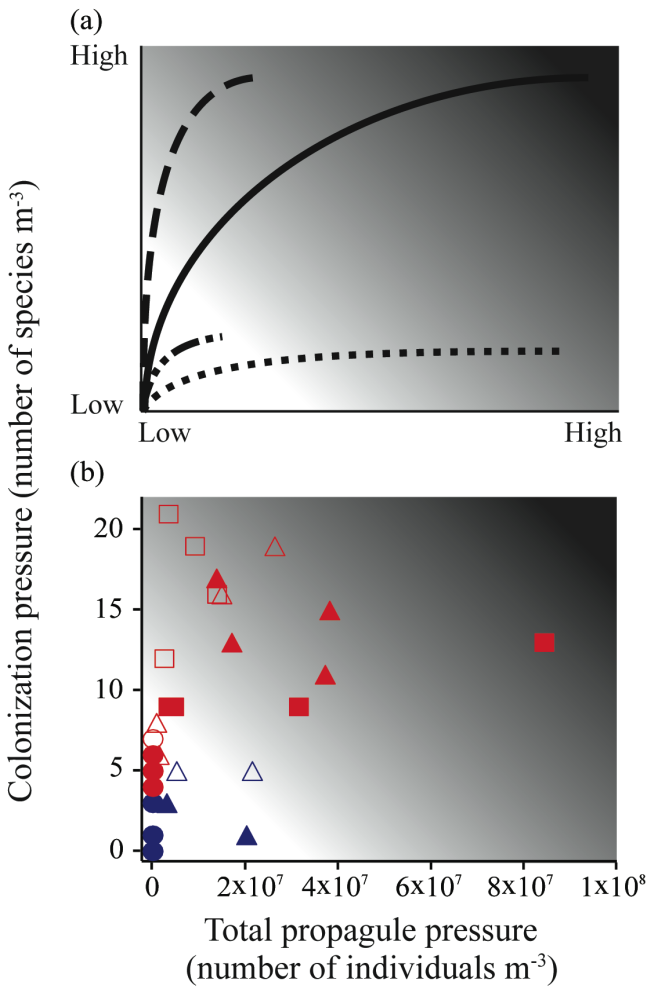

Figure 5.1 Conceptual model (a) of the relationship between colonization pressure (CP) and total propagule pressure (total PP) for species assemblages translocated by a transport vector under four different scenarios: high CP and total PP for species-rich and high-abundance assemblages (solid line); high CP and low total PP for species-rich assemblages with low abundance of most or all species (dashed line); low CP and high total PP for species assemblages with at least one abundance species (dotted line); and low CP and total PP for assemblages represented by a few species in low numbers (dotted-dashed line). Final CP and total PP (b) for invertebrate (circles; n = 16), diatom (triangles; n = 14), and dinoflagellate (squares; n = 4) assemblages at the end of two

trans-Atlantic (blue) and two trans-Pacific (red) voyages. Solid and open markers denote assemblages collected from control and exchanged tanks, respectively. Background shading in both panels indicates relative introduction risk with light, medium, and dark shadings representing relatively low, moderate, and high risk, respectively.

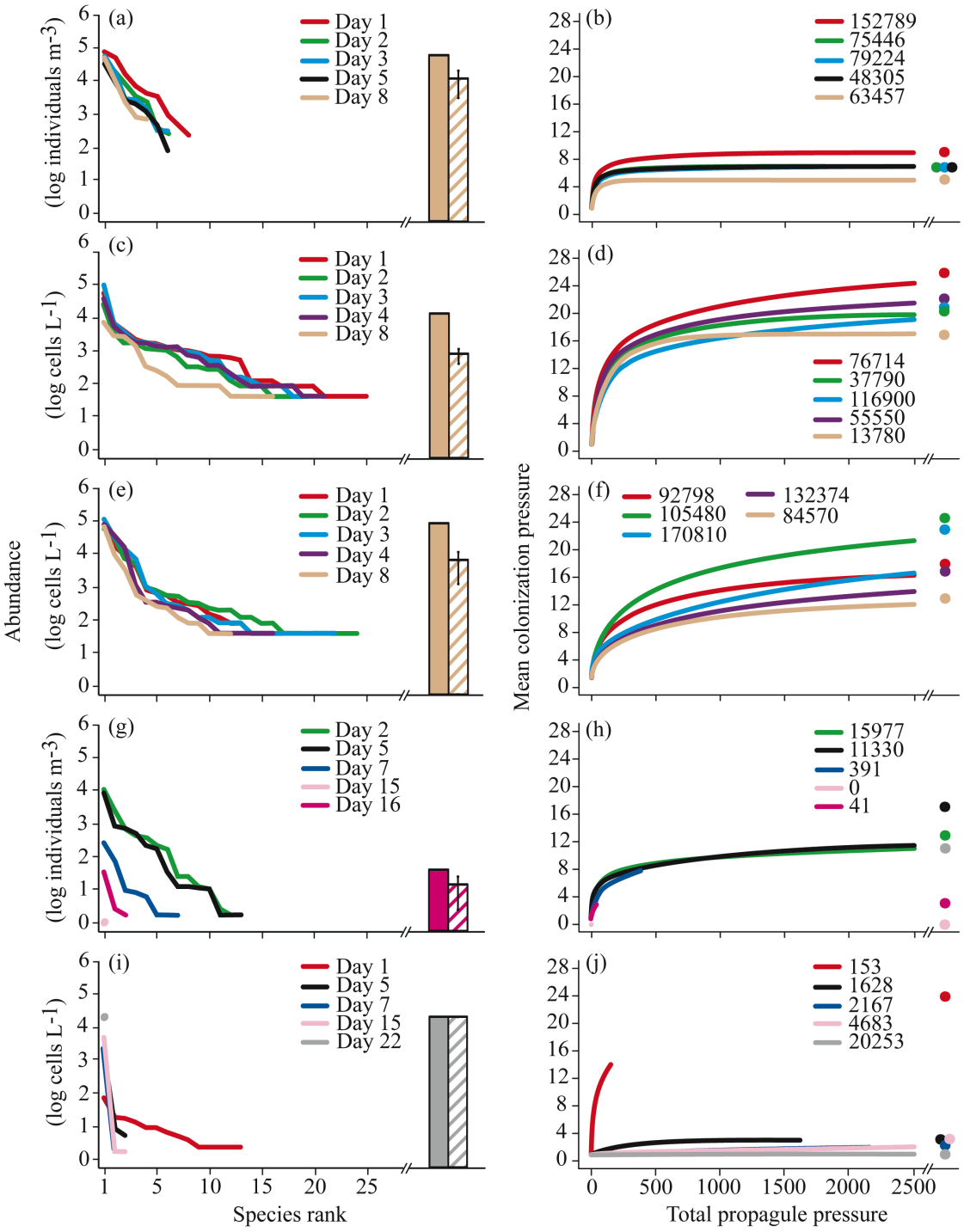

Figure 5.2 Rank-abundance distributions (left panels) and corresponding colonization pressure:total propagule pressure curves (CP:total PP; right panels) illustrating changes in the structure of plankton assemblages in unexchanged ballast water of ships during trans-

Atlantic (a-f) and trans-Pacific (g-j) voyages. Panels (a), (b), (g), and (h) show results for invertebrates; (c), (d), (i), and (j) for diatoms; and (e) and (f) for dinoflagellates. Samples for different taxonomic groups were collected from the same tank and ship for each voyage. The five lines on each graph depict the rank-abundance distributions or CP:total PP relationships on five different days. Colour scheme for different days of the voyages applies to the entire figure. Also shown in each left panel are total PP (solid bar) and mean PP (± S.E.M; hatched bar) recorded at the last time point. Numeric values and circles in each right panel indicate observed total PP and estimated asymptotic species richness (Chao-1). Circles are offset when values overlap.

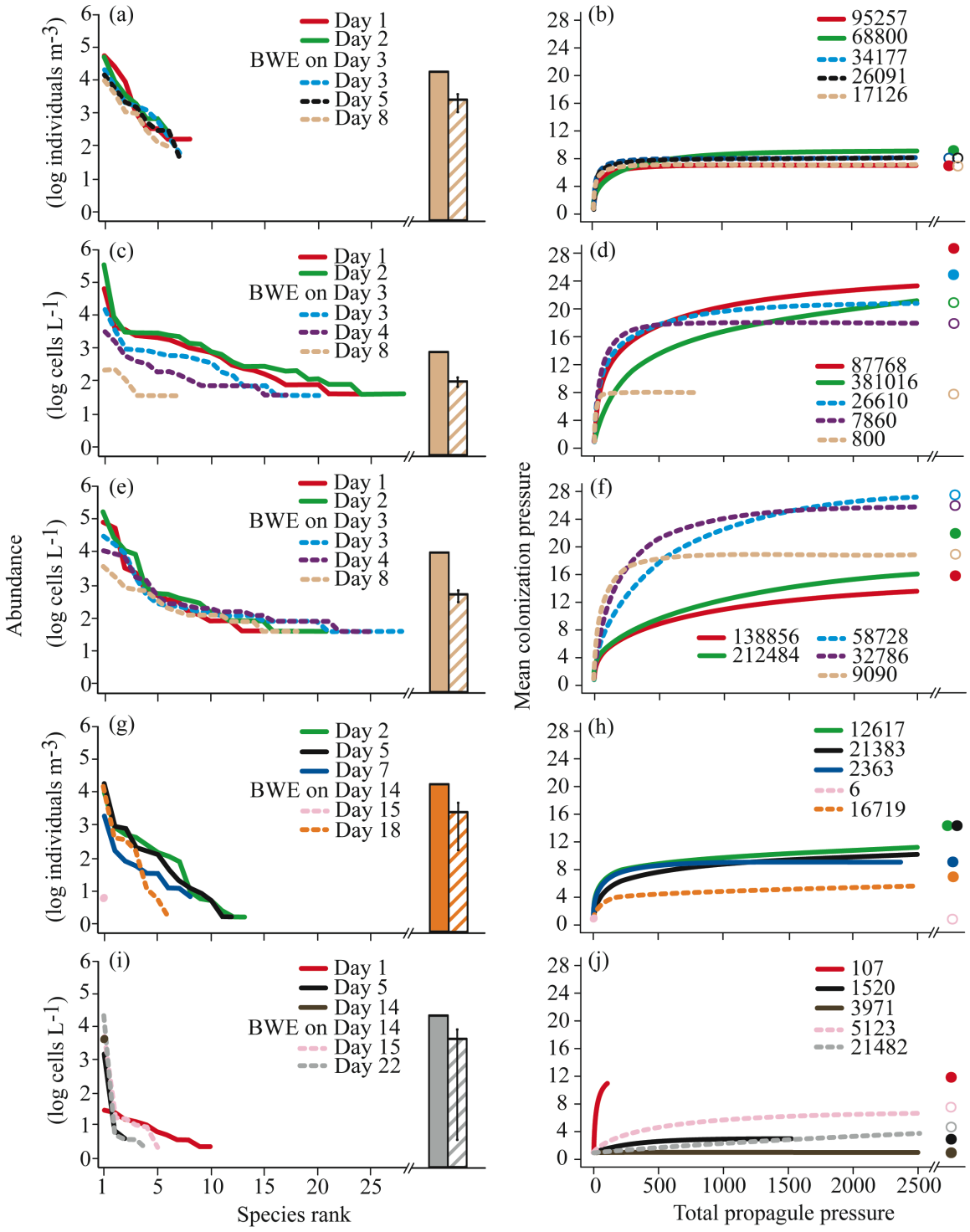

Figure 5.3 Rank-abundance distributions (left panels) and corresponding CP:total PP curves (right panels) highlighting changes in the structure of plankton assemblages in ships' ballast water before and after ballast water exchange during trans-Atlantic (a-f) and

trans-Pacific (g-j) voyages. Panels (a), (b), (g), and (h) show results for invertebrates; (c), (d), (i), and (j) for diatoms; and (e) and (f) for dinoflagellates. Samples for different taxonomic groups were collected from the same tank and ship (paired-tank of the same ship as figure 2) for each voyage. Solid and dotted lines indicate results before and after ballast water exchange, respectively. Descriptions of symbols used are given in Figure 5.2.

5.5 Supplementary Information

Table S5.1 Results of linear mixed-effects models testing the fixed effects of time, quadratic term of time (time^2), ballast water exchange (BWE) status, and the interaction term between time and BWE status (time × BWE status) for colonization pressure and total propagule pressure associated with invertebrate and diatom assemblages in control and exchanged tanks during trans-Atlantic and trans-Pacific voyages after BWE. Time was defined as the number of days since BWE. Time × BWE status was not retained in any model. Dashes (-) indicate non-significant variables that were excluded in the final optimal models.

	Invertebrates				**Diatoms**			
	d.f.	β	t	p	d.f.	β	t	p
Colonization pressure (Atlantic)								
Time	36	-0.2	-2.1	0.04	-	-	-	-
Time^2	-	-	-	-	-	-	-	-
BWE status	36	1.9	5.2	<0.01	-	-	-	-
Total propagule pressure (Atlantic)								
Time	36	-2083.5	-2.8	<0.01	30	-2061.1	-2.0	0.05
Time^2	-	-	-	-	-	-	-	-
BWE status	36	-25360.5	-7.3	<0.01	30	-21832.5	-2.2	0.03
Colonization pressure (Pacific)								
Time	20	1.3	5.0	<0.01	14	-0.3	-7.2	<0.01
Time^2	-	-	-	-	-	-	-	-
BWE status	20	2.1	3.4	<0.01	-	-	-	-
Total propagule pressure (Pacific)								
Time	-	-	-	-	16	-5485.3	-2.7	0.02
Time^2	-	-	-	-	16	683.3	3.1	<0.01
BWE status	-	-	-	-	-	-	-	-

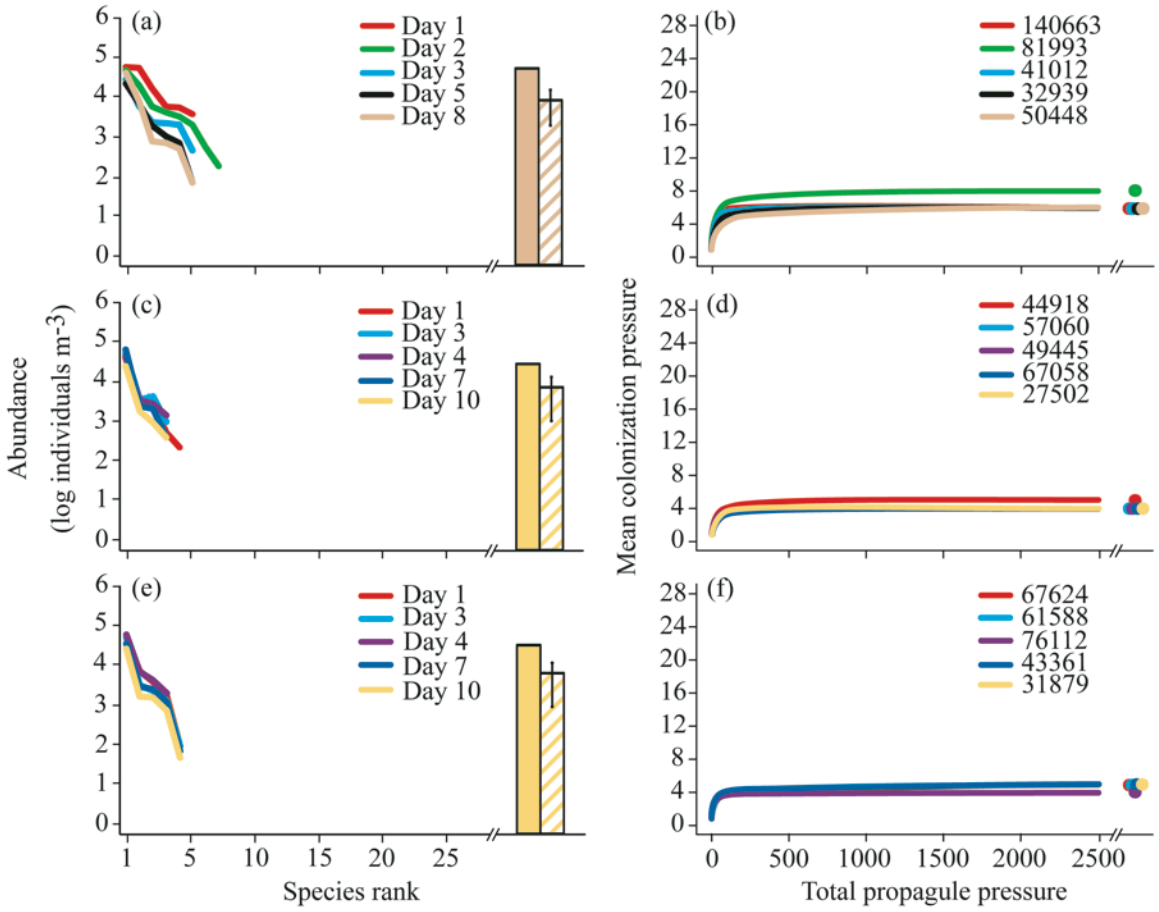

Figure S5.1 Rank-abundance distributions (left panels) and corresponding colonization pressure:total propagule pressure curves (CP:total PP; right panels) highlighting changes in the structure of invertebrate assemblages in unexchanged ballast water of ships during trans-Atlantic voyages. The five lines on each graph depict rank-abundance distributions of CP:total PP relationships on five different days. Colour scheme for different days of the voyages applies to the entire figure. Also shown in each left panel are total PP (solid bar) and mean PP (± S.E.M; hatched bar) recorded at the last time point. Numeric values and circles in each right panel indicate observed total PP and estimated asymptotic species richness (Chao-1). Circles are offset when values overlap.

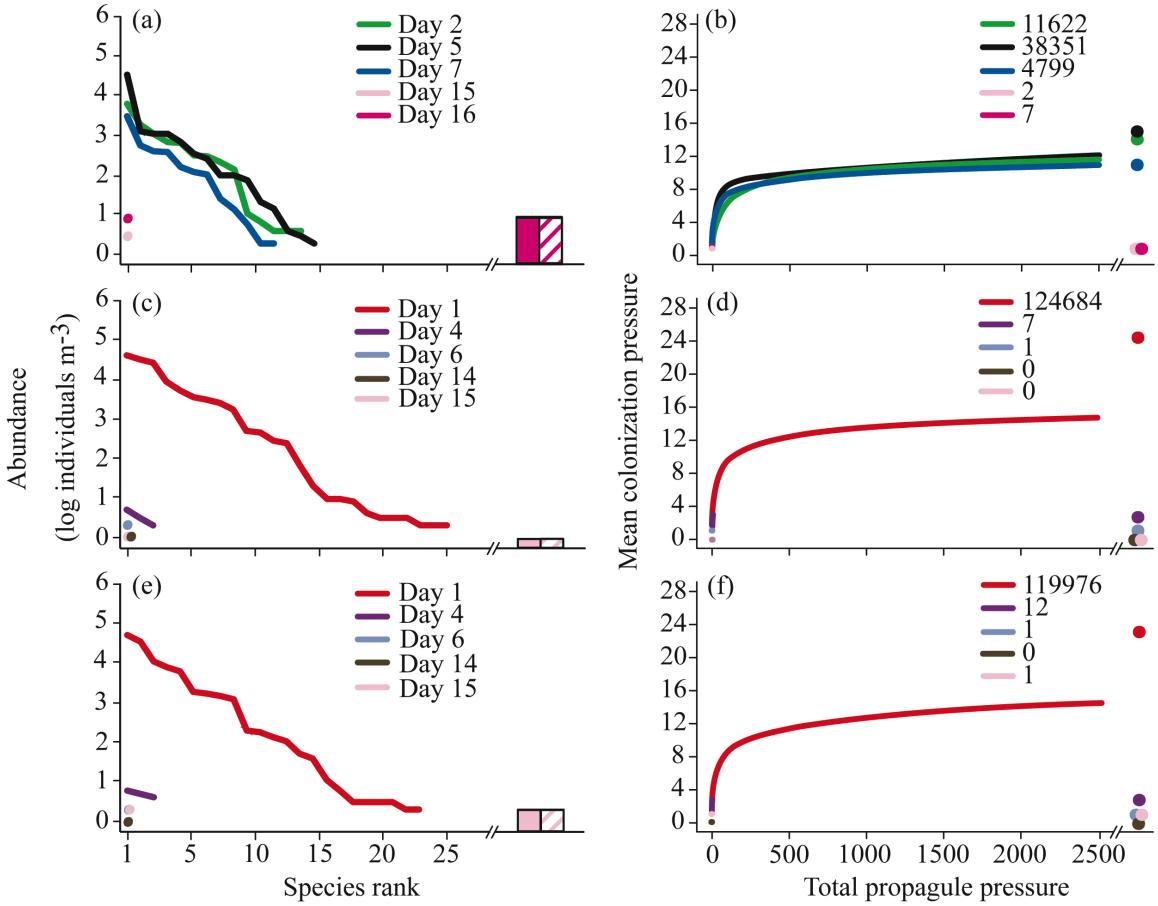

Figure S5.2 Rank-abundance distributions (left panels) and corresponding CP:total PP curves (right panels) showing changes in the structure of invertebrate assemblages in unexchanged ballast water of ships during trans-Pacific voyages. Descriptions of symbols used are given in Supplementary Figure S5.1.

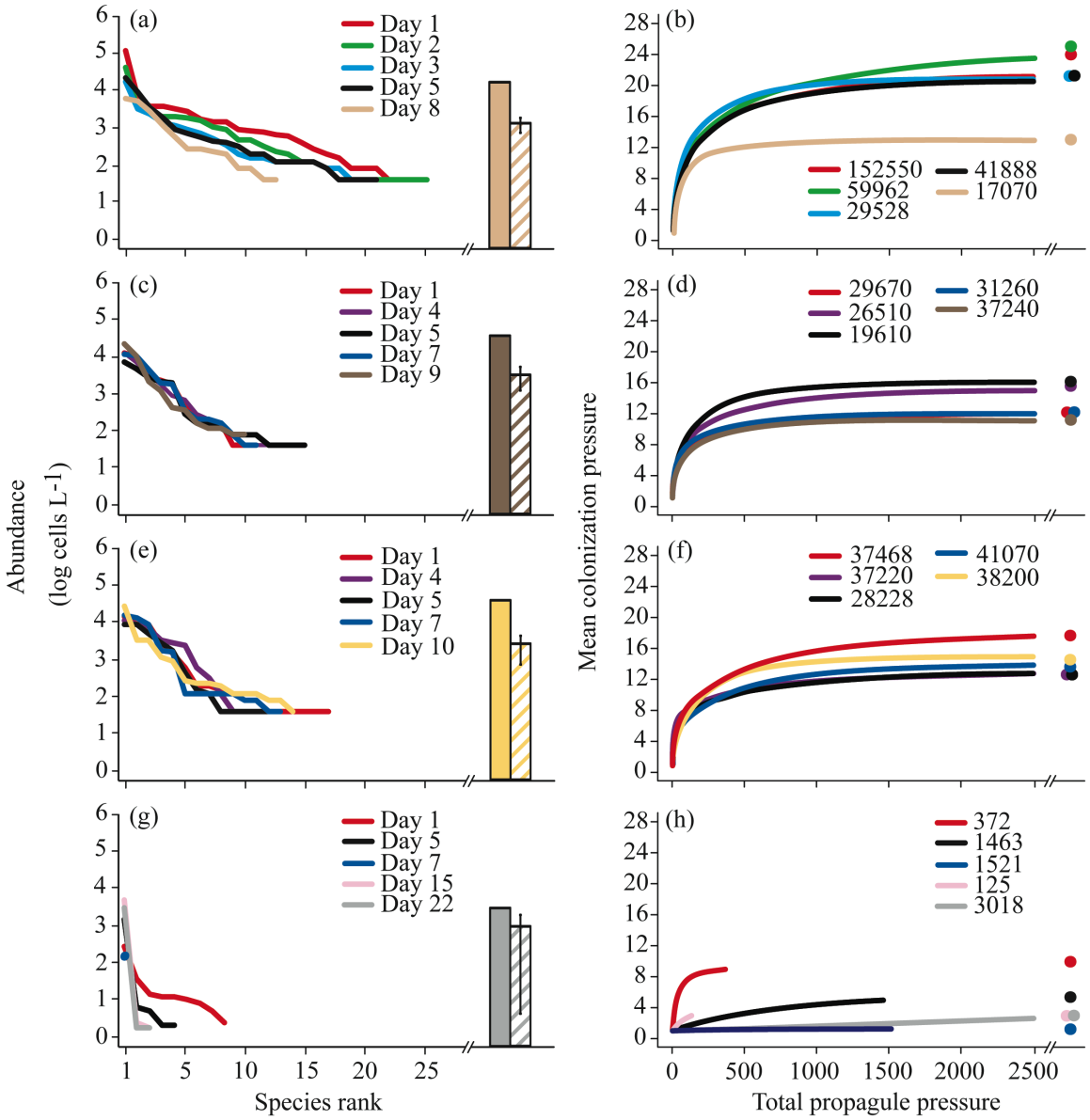

Figure S5.3 Rank-abundance distributions (left panels) and corresponding CP:total PP curves (right panels) illustrating changes in the structure of diatom assemblages in unexchanged ballast water of ships during trans-Atlantic (a-f) and trans-Pacific (g-h) voyages. Descriptions of symbols used are given in Supplementary Figures S5.1.

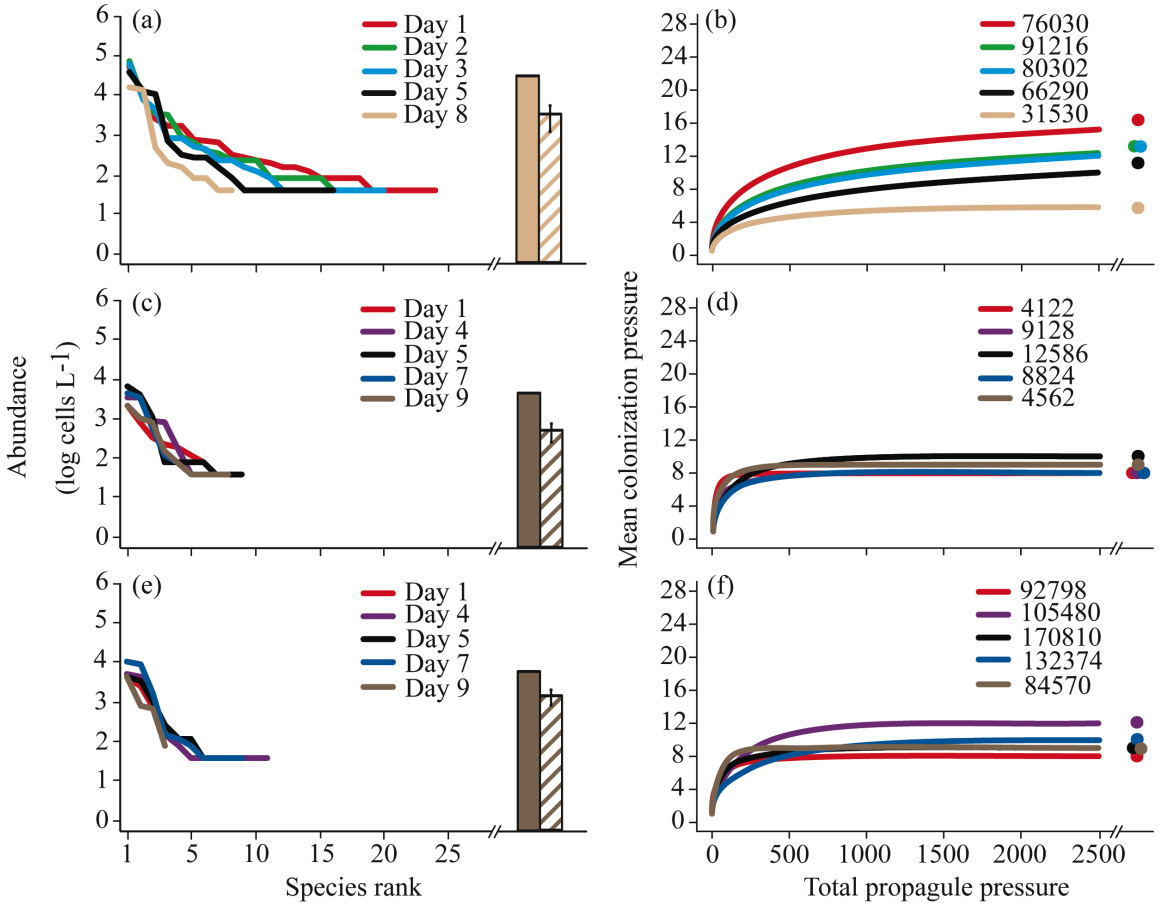

Figure S5.4 Rank-abundance distributions (left panels) and corresponding CP:total PP curves (right panels) demonstrating changes in the structure of dinoflagellate assemblages in unexchanged ballast water of ships during trans-Atlantic voyages. Descriptions of symbols used are given in Supplementary Figure S5.1.

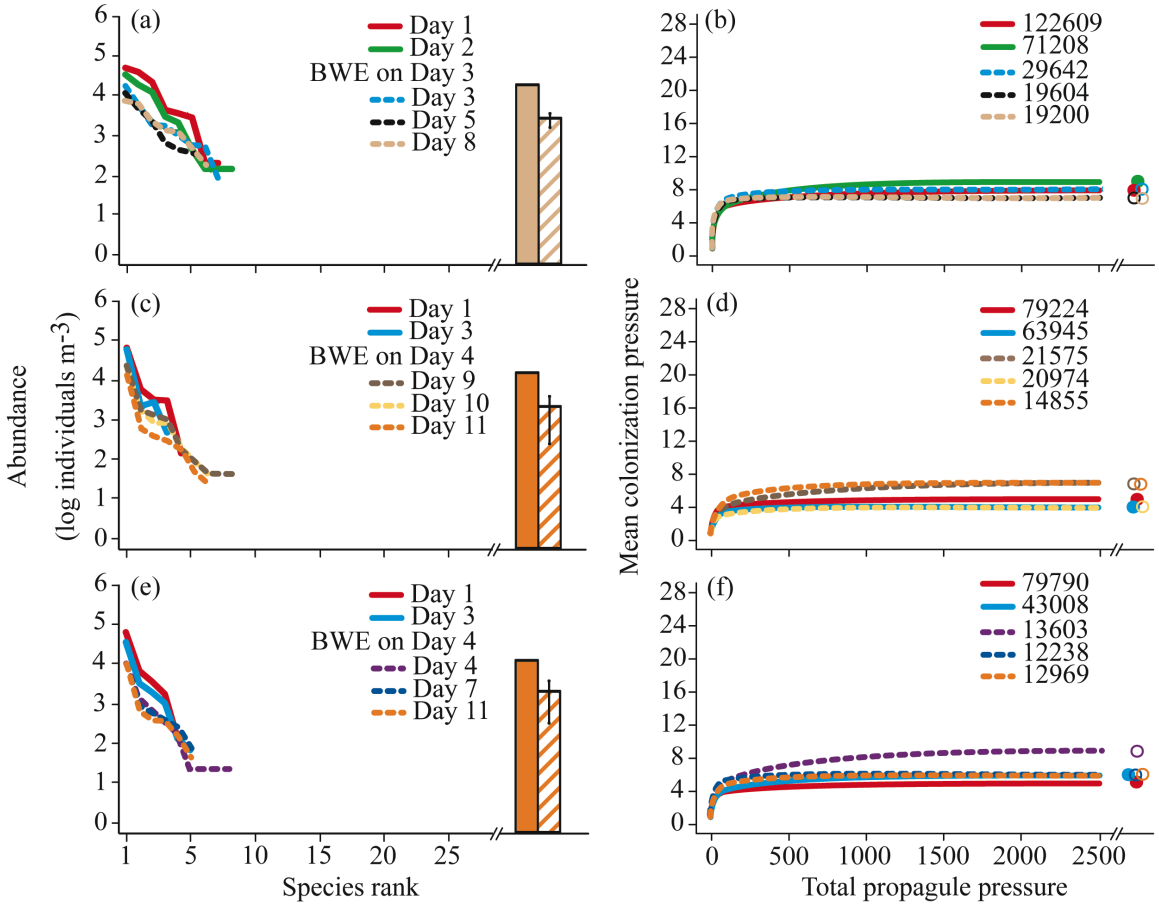

Figure S5.5 Rank-abundance distributions (left panels) and corresponding CP:total PP curves (right panels) highlighting changes in the structure of invertebrate assemblages in ships' ballast water before and after ballast water exchange during trans-Atlantic voyages. Descriptions of symbols used are given in Supplementary Figure S5.1.

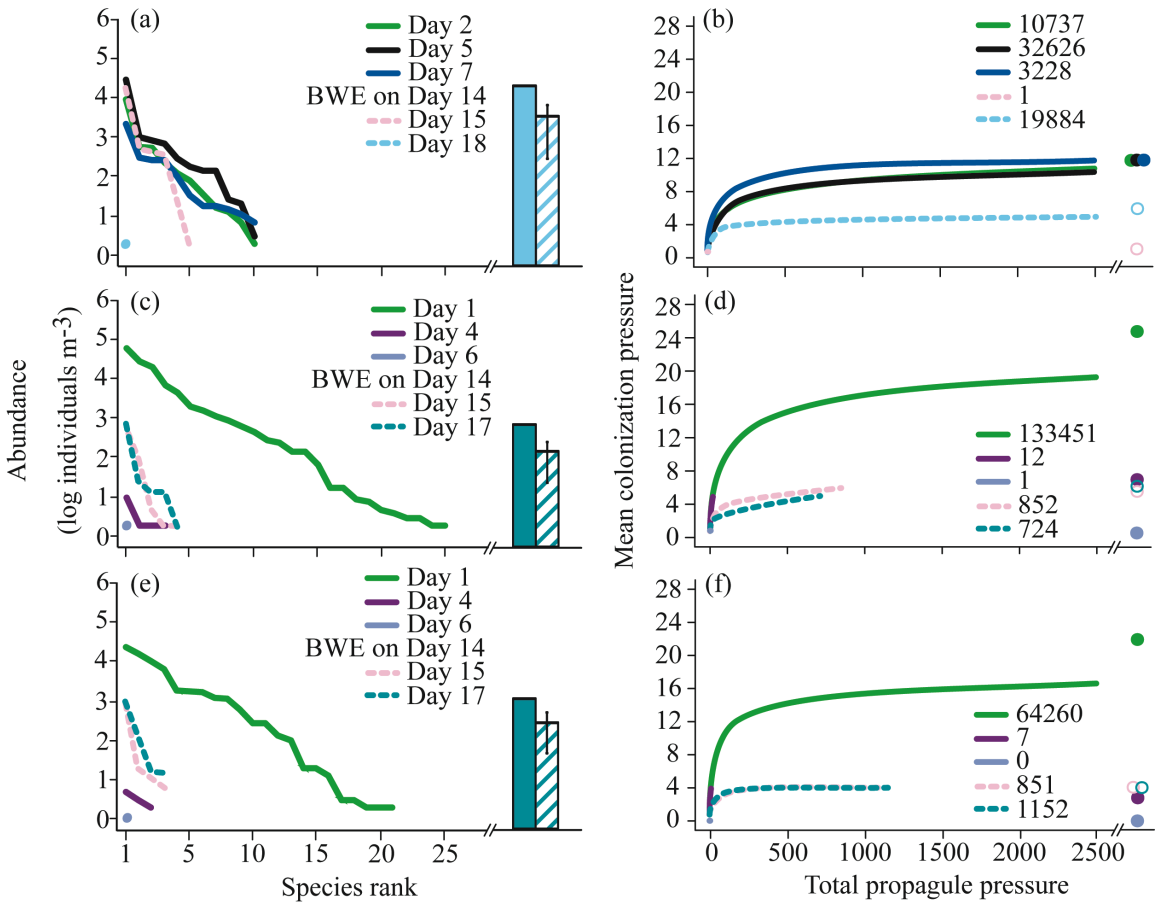

Figure S5.6 Rank-abundance distributions (left panels) and corresponding CP:total PP curves (right panels) illustrating changes in the structure of invertebrate assemblages in ships' ballast water before and after ballast water exchange during trans-Pacific voyages. Descriptions of symbols used are given in Supplementary Figure S5.1.

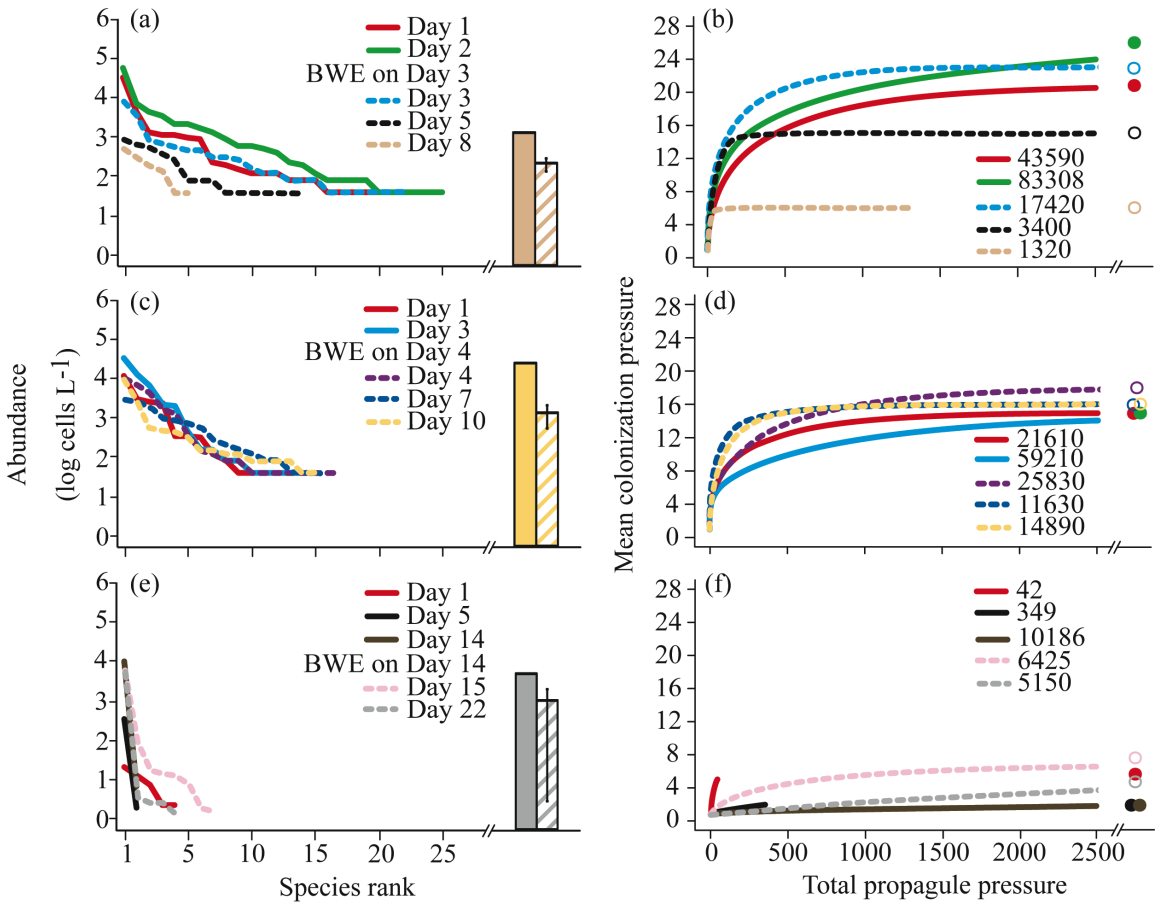

Figure S5.7 Rank-abundance distributions (left panels) and corresponding CP:total PP curves (right panels) demonstrating changes in the structure of diatom assemblages in ships' ballast water before and after ballast water exchange trans-Atlantic (a-d) and trans-Pacific (e-f) voyages. Descriptions of symbols used are given in Supplementary Figure S5.1.

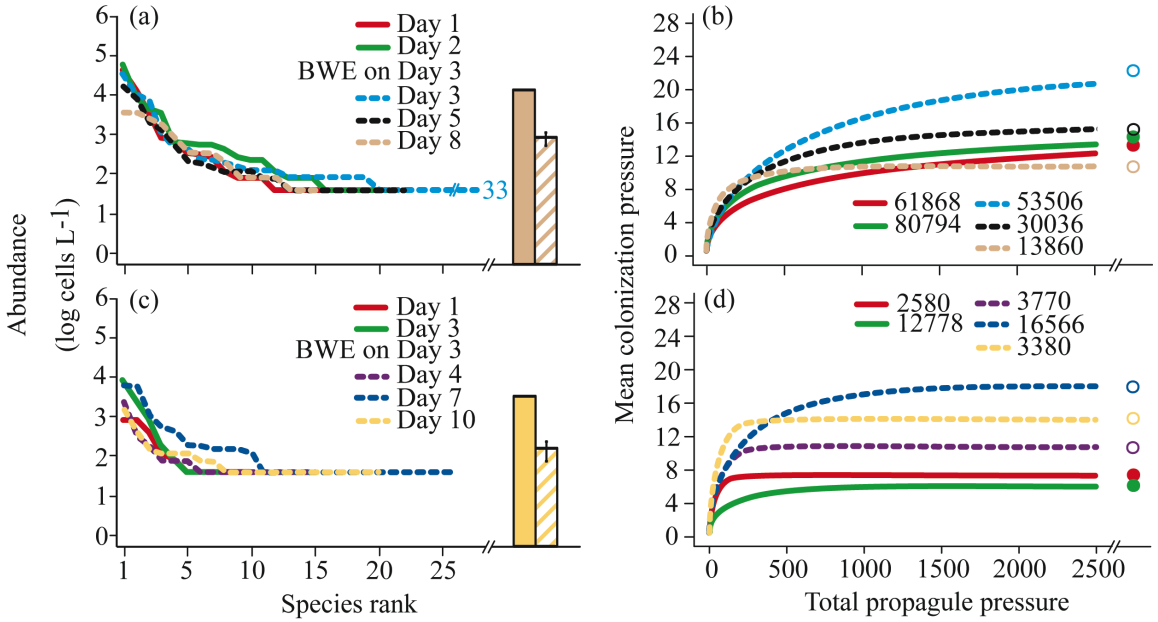

Figure S5.8 Rank-abundance distributions (left panels) and corresponding CP:total PP curves (right panels) showing changes in the structure of diatom assemblages in ships' ballast water before and after ballast water exchange trans-Atlantic voyages. Descriptions of symbols used are given in Supplementary Figure S5.1.

CHAPTER 6: GENERAL DISCUSSION

In this dissertation, I have provided the first comprehensive evaluation of ship-mediated nonindigenous species (NIS) invasion risk in the Canadian Arctic. My vector-based risk assessment indicates that the Port of Churchill is at greatest invasion risk because it receives the largest volume of ballast water discharged by international merchant vessels and because its environmental conditions broadly match those of connected global and domestic ports that contain high-impact NIS (Chapter 2). Biological surveys that examined species assemblages transported in ballast water and on hulls of vessels arriving at Churchill reveal that both ballast water and hull fouling are active vectors for transferring marine species to the Canadian Arctic, but the latter appears to be the more important vector for delivery of NIS (Chapters 3 and 4). The discovery of viable nonindigenous barnacles on vessel hulls provides the first record of temperate fouling NIS surviving transit to a sub-Arctic port, highlighting the importance of hull fouling as a transport vector of NIS (Chapter 4). Additionally, I have contributed novel insights into the characteristics and mechanisms of human-assisted dispersal of NIS to the Canadian Arctic and elsewhere (Chapters 3 and 5). I found that community structure and the relationship between colonization pressure (CP) and total propagule pressure (total PP) of species assemblages in ballast water vary over time during transport (Chapter 5). Final species rank-abundance distributions and CP:total PP relationships of entrained assemblages are dependent on transit pathway (i.e. ballast water age/voyage length and source region), taxonomic group (i.e. invertebrates, diatoms, and dinoflagellates), and vector management strategy (i.e. ballast water exchange) (Chapters 3 and 5).

6.1 Ship-mediated invasion risk in the Canadian Arctic

A challenging aspect in addressing biological invasions is to quantify and forecast invasion risks associated with vectors transporting large, unknown species assemblages (Ruiz and Carlton 2003; Wonham et al. 2013). I developed and demonstrated the use of a predictive, vector-based risk assessment framework to assess relative ballast-mediated invasion risk at Canadian Arctic ports (Chapter 2). The framework determined relative invasion risks between shipping pathways by quantifying the probability of NIS successfully overcoming all stages of the invasion process and the magnitude of potential consequences of introduction to Arctic ports based on ballast water patterns, environmental similarity between port-pairs, and the number of high-impact NIS in connected source regions. Results of the risk assessment can be useful for directing research and proactive management efforts at potentially high-risk sites (e.g. Churchill) and shipping pathways (e.g. international merchant vessels). These findings led me to focus sampling efforts on vessels visiting Churchill (Chapters 3 and 4). My results have also directed biodiversity surveys at Churchill and other high-risk ports to establish a baseline for early detection and monitoring of NIS (Goldsmit et al. 2014).

While the risk assessment framework can be applied to other vectors, I did not adopt it for hull fouling because appropriate proxy measures for hull fouling PP were not available. I considered using the number or wetted surface area of vessels that had arrived at Arctic ports – data that are readily available from most shipping databases – as proxy measures for PP associated with hull fouling (see Davidson et al. 2006; Lo et al. 2012). However, numerous studies have found that total PP varies widely across vessels depending on a large number of factors, including voyage history, port residence time,

sailing speed, time since last dry-dock, and age and type of anti-fouling paint; thus the number of vessel arrivals is a poor proxy measure for PP (e.g. Davidson et al. 2009; Coutts et al. 2010; Sylvester and MacIsaac 2010; Sylvester et al. 2011). Wetted surface area is not a reliable proxy variable for PP either because fouling tends to accumulate on niche areas such as propeller and rudder, independent of the total colonizable space available on vessels (Coutts and Taylor 2004; Davidson et al. 2009; Sylvester and MacIsaac 2010; Chapter 4). Furthermore, fouling species accumulate on vessel hulls from various sources over time (see Chapman et al. 2013). It was, therefore, impossible to identify point sources of potential fouling NIS to compare environmental conditions between port-pairs and to determine the number of high-impact NIS at connected regions. Nevertheless, the risk assessment framework should be suitable for vectors that have appropriate proxy measures for PP and identifiable localized sources of potential NIS.

The ability to determine the relative importance of multiple, simultaneous vectors allows management efforts to be targeted at the vector that poses the greatest risk given limited managerial resources. Previously, the relative importance of ship vectors have been evaluated by assigning established NIS to one or more possible vectors based on species' life-history characteristics, habitat(s) of occurrence, and mobility (e.g. Fofonoff et al. 2003a; Ruiz et al. 2011; Williams et al. 2013). This approach is problematic as many NIS could have been introduced via multiple vectors, including non-ship vectors (e.g. aquaculture) (Fofonoff et al. 2003a; Williams et al. 2013). A small number of studies have directly sampled ship fouling (e.g. Gollasch 2002b; Lewis et al. 2003; Sylvester et al. 2011), but my study is the first to quantitatively compare CP and/or total PP transported by multiple vectors on the same vessels. Findings of Chapter four suggest

that hull fouling is a more important transport vector than ballast water for delivering marine NIS to the Canadian Arctic. While I did not find significant differences in total PP and CP for NIS between vectors within the same vessels, likely owing to the small sample size, both nonindigenous total PP and nonindigenous CP were significantly higher for hull fouling than for ballast water when comparing vectors across vessels. In addition, a positive relationship between nonindigenous CP and nonindigenous total PP for hull fouling indicates that more heavily fouled vessels tended to transport a greater number of NIS; such a relationship was not found for ballast water.

Comparisons of results from my biological surveys of ship vectors with those from other studies reveal that ballast water generally delivers lower CP and total PP to the Arctic than to the Atlantic and Pacific coasts of Canada (DiBacco 2007b, 2007c, 2008; Table 6.1). Lower CP but higher total PP are typically transferred to the Arctic via ballast water when compared to the Great Lakes (DiBacco 2007d; Table 6.1). The vector appears to deliver similar CP to both the Canadian Arctic and the Antarctic (Lewis et al. 2003; Table 6.1); I was not able to compare total PP transferred because this information was not available for the Antarctic. In the case of hull fouling, lower CP but higher total PP are generally transported to the Canadian Arctic than to most temperate regions (Sylvester et al. 2011; Table 6.1). However, this finding was highly influenced by two densely fouled vessels in the Arctic, which, if removed, would have resulted in similar CP and total PP transported as found in most instances in the Great Lakes (Sylvester and MacIsaac 2010), and a much lower instance than the extreme case described by Drake and Lodge (2007) (Table 6.1). Comparable CP is transferred to the Canadian Arctic and the Antarctic via hull fouling (Lewis et al. 2003, 2006; Lee and Chown 2009; Table 6.1).

Again, I was not able to compare total PP delivered to the two polar regions. However, Lewis et al. (2006) reported an estimated total abundance of 1.4×10^5 for three species out of the 20 fouling taxa found on a barge surveyed at a sub-Antarctic island, suggesting that total PP transported to the Antarctic via hull fouling may be quite high (Table 6.1). It is important to note that these comparisons were made based on CP and total PP transported during a single introduction event.

The overall ship-mediated invasion risk in the Canadian Arctic may be relatively low because it currently receives less traffic and a smaller volume of ballast water discharge than most regions, and because the environment remains inhospitable for many temperate species. For example, the volume of ballast water discharged in the region is 0.4%, 1.5%, and 0.8% of that in the Great Lakes-St. Lawrence River, and Atlantic and Pacific regions of Canada, respectively (Casas-Monroy et al. 2014). Canada's Arctic also has less vessel traffic than other Arctic regions, with approximately 10% and 12% of the number of vessel arrivals in Alaska and Greenland, respectively (McGee et al. 2006; Arctic Council 2009; Gill 2014). While shipping data were not available for the Antarctic for a quantitative comparison, the risk of introducing NIS to the region via ballast water is considered very low owing to minimal commercial ship traffic (Lewis et al. 2003). However, the risk of introducing hull-borne NIS to the Antarctic via tour and research vessels may be high (Lewis et al. 2003, 2006; Lee and Chown 2009). Indeed, hull fouling has been suggested as the vector responsible for the introduction of the nonindigenous green alga *Enteromorpha intestinalis* to the Antarctic (Frenot et al. 2009).

6.2 Understanding mechanisms of human-assisted species dispersals

Owing to their physical characteristics, many transport vectors such as ships' ballast water or fouled hulls, bait worm packaging, and wood dunnage have the potential to translocate large, mixed-species assemblages during a single human-mediated movement (e.g. Briski et al. 2013; Haack et al. 2014; Haska et al. 2014). Understanding the relationship between CP and total PP for species assemblages transported by these vectors can improve our ability to forecast invasions by identifying conditions where high-risk (i.e. high CP, high total PP, or both) introduction events can be expected (Lockwood et al. 2009; Briski et al. 2012, 2014). I determined that CP:total PP relationships for invertebrate assemblages in ballast water were influenced by ballast water age (Chapter 3). I found a significantly positive relationship between CP and total PP for invertebrates in older ballast water (~5 days), indicating that CP and total PP decreased proportionately as ballast water aged. In contrast, the absence of such a relationship for invertebrates in younger ballast water (~7 days) suggests that decreases in total PP were accompanied by little to no reduction in CP. Collectively, these results suggest that invasion risk of invertebrates in younger ballast water is higher than that in older ballast water. These findings led me to investigate temporal changes in the CP:total PP relationship for species assemblages transported by ballast water.

Analysing how assemblage structure varies during transport can provide insights into how introduction risk changes before propagules are released (Briski et al. 2014). I demonstrated the application of rank-abundance distributions in invasion ecology to examine how CP:total PP relationships change temporally in ballast water of ocean-going

ships (Chapter 5). I found that rank-abundance distributions and CP:total PP patterns varied vary widely between trans-Atlantic and trans-Pacific voyages, with the latter appearing to pose a much lower risk than the former. The effects of voyage route may be due to differences in source inocula and voyage length (Gollasch et al. 2000b, Verling et al. 2005; Cordell et al. 2009; Briski et al. 2012, 2013). Responses also differed by taxonomic group, with invertebrates experiencing losses mainly in total PP, while diatoms and dinoflagellates sustained losses predominantly in CP. Relative dynamics for CP and total PP among taxonomic groups may be attributed to taxon-specific tolerance to abiotic and biotic stresses (Briski et al. 2014). In certain cases, open-ocean ballast water exchange appeared to increase introduction risk by uptake of new species or supplementation of existing ones. Additionally, I demonstrated that rank-abundance distributions provide a more accurate description of entrained assemblages than summary statistics including total and mean PP. Rank-abundance distributions effectively characterize variation in abundance across species, making it possible to visualize and examine assemblage dynamics (e.g. changes in abundance of particular species) over time, particularly before and after vector management, thereby allowing refined estimation of introduction risk.

6.3 Future work

Results presented here are based on current shipping and ballast water discharge patterns as well as environmental conditions. Any changes to one or both factors in the future will lead to changes in invasion risk associated with ship vectors. To improve our ability to forecast future ship-mediated invasions, I propose extending the vector-based

risk assessment framework in Chapter 2 to include modelling work that can project future shipping traffic based on proposed development and/or environmental conditions under various climate change scenarios (e.g. Floerl et al. 2013; Ware et al. 2013). Developing new or modifying current risk assessment frameworks to assess invasion risk associated with hull fouling should also be a priority given its relative importance as a transport vector of NIS in the Canadian Arctic and other coastal ecosystems (e.g. Hewitt et al. 2009; Farrapeira et al. 2011; Gollasch 2002b; Chapter 4).

In addition, this dissertation has improved our knowledge of human-mediated transport mechanisms via multi-species vectors by identifying factors that influence community structures and CP:total PP patterns of entrained assemblages (Chapter 5). The next step is to develop models to understand the relationship between invasion risk and CP:total PP, especially for species assemblages introduced via unintentional transport such as ballast water and hull fouling. Descriptive and mechanistic models have been developed to predict invasions of a single species or a suite of known species (e.g. Gertzen et al. 2011; Bradie et al. 2013; Brockerhoff et al. 2014). These models may be adaptable to predict invasions of large, unknown species assemblages (Wonham et al. 2013).

In the case of ballast water, the modelling work may provide a risk assessment methodology to evaluate concentration-based numeric discharge limits, such as the D-2 Ballast Water Performance Standard proposed by the International Maritime Organization and others proposed by various countries and states/territories (IMO 2004; Albert et al. 2013). These discharge standards seek to prevent new invasions by reducing the number of organisms in ballast water via effective ballast water treatment

technologies (IMO 2004). These standards, however, focus only on total PP and do not differentiate discharges between single and multiple species (i.e. low to high CP). Ballast water that meets a certain discharge standard may pose varying level of risk depending on the underlying species rank-abundance distribution of entrained assemblages. For example, for a sample of 1,000 organisms (i.e. total PP = 1,000), a highly skewed rank-abundance distribution could occur such that the assemblage is characterized by few species (i.e. low CP) with the dominant ones occurring at high abundance (Drake et al. 2014). If introduced into a suitable environment, probability of establishment of the dominant species may be high, resulting in successful invasions. In contrast, for the same sample of 1,000 organisms, a strongly even rank-abundance distribution would comprise many species (i.e. high CP) but each presenting in low numbers (Drake et al. 2014). Probability of establishment of all species may be low because of demographic constraints, even if they are introduced into a suitable habitat. Understanding the relationship between invasion risk and CP:total PP will increase our ability to forecast changes in invasion risk associated with each proposed standard as many countries, including Canada, are planning to adopt a concentration-based numeric discharge standard as a means to manage ballast water.

Table 6.1 Comparison of colonization pressure (CP) and total propagule pressure (total PP) transported to the Canadian Arctic, the Atlantic and Pacific coasts of Canada, the Great Lakes, and the Antarctic in ballast water and on vessel hulls. Values are averaged across ships. Sample size and data sources are also included. Total PP data are not available for the Antarctic.

	CP (taxa ship^{-1})	Total PP (individuals ship^{-1})	Sample size	Data sources
Ballast water				
Arctic	5	1.7×10^{7}	32	Chapter 4
Atlantic	15	5.5×10^{8}	58	DiBacco 2007b
Pacific	15	6.3×10^{7}	60	DiBacco 2007c, 2008
Great Lakes	11	4.2×10^{5}	20	DiBacco 2007d
Antarctic	5	n.a.	4	Lewis et al. 2003
Hull fouling				
Arctic	11	4.9×10^{5}	13	Chapter 4
	10	1.7×10^{5} (outliers removed)	11	Chapter 4
Atlantic	15	2.7×10^{4}	20	Sylvester et al. 2011
Pacific	50	9.4×10^{4}	20	Sylvester et al. 2011
Great Lakes	11	1.7×10^{5}	20	Sylvester and MacIsaac 2010
	74	1.7×10^{6}	1	Drake and Lodge 2007
Antarctic	20	1.4×10^{5} (based on 3 species only)	1	Lewis et al. 2006
	17	n.a.	3	Lewis et al. 2003
	8	n.a.	1	Lee and Chown 2009

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